POLLEN MORPHOLOGY OF THE LEONTODONTINAE (ASTERACEAE:LACTUCEAE)

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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NY The New York Botanical Garden

US U. S. National Herbarium, Smithsonian Institution

GH Gray Herbarium, Harvard University

F Field Museum of Natural History, Chicago

INTRODUCTION

The tribe Lactuceae (Cichorieae) of the Asteraceae (Compositae) includes approximately 72 genera and 2300 species. The Lactuceae has 3 main centers of distribution: central Asia, the Mediterranean Basin, and western North America. The tribe was first recognized as a natural group by de Jussieu (1789) and has since come to be considered the most distinctive tribe of the Asteraceae, sharply defined by its ligulate heads, milky sap, and the widespread occurrence of highly sculptured, echinolophate pollen.

This study examines the pollen characters of the subtribe Leontodontinae (Garhadiolus, Hedypnois, Hypochoeris, Leontodon, Picris, Rhagadiolus, Urospermum) of Stebbins (1953). Because Jeffrey (1966) linked Aposeris and Hyoseris with the Leontodontinae on the basis of microcharacters, the pollen of these two genera also will be considered to ascertain if pollen data can be used to support Jeffrey's disposition of them.

This thesis describes and documents endo- and exomorphological pollen data of the subtribe using light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). These data are used to ascertain the relative degree of cohesiveness or naturalness of the subtribe and to improve the general understanding of cichoriacious pollen. The utility of pollen morphology in determining generic limits is also discussed.

LITERATURE REVIEW

Students of the Lactuceae have traditionally found the tribe to be taxonomically difficult because of the paucity of distinguishing exomorphic floral characters. Early synantherologists found the nature of the pappus to be the single most useful diagnostic character and based their classifications largely on pappus and achene characters. This practice produced highly artificial treatments of the Lactuceae (de Jussieu, 1789; Don, 1825; Cassini, 1826; Lessing, 1832; DeCandolle, 1838; Bentham, 1873a, 1873b; Hoffman, 1891). Modern systematists have been able to develop more natural classifications because 20th century tools and techniques have revealed new taxonomically useful characters. Stebbins (1953) emphasized pollen, stigmatic, and chromosomal characters in conjunction with phytogeography and growth habits to cluster the genera into 8 subtribes which are generally acknowledged as more natural than previous groupings. Jeffrey (1966) modified Stebbins' scheme using floral microcharacters (size and shape of collecting hairs on the style and style arms, and type of pubescence on the exterior of the corolla tube) to separate the tribe into 5 groups, 11 subgroups and 23 series. Formal taxonomic status was not given to these groups because Jeffrey recognized the need for further study, and was undecided as to what status (tribal or subfamilial) should be accorded the ligulate Asteraceae.

Pollen characters were not easily incorporated into systematic investigations into the Lactuceae or other taxa until relatively recently but the study of pollen is by no means a modern science. Its development has indeed progressed markedly with 20th century advances in light and electron microscopy, but centuries before the first optics were ground, man was curiously aware of this yellow dust that forms inside flowers.

The Latin word pollen (noun, neuter, 3rd declension) does in fact mean a fine flour or dust. Curiosity about pollen developed into genuine interest when 17th century microscopists Nehemiah Grew and Marcello Malphigi first described variations between pollen grains of different species, thereby laying the cornerstone for the field of systematic palynology. In 1694 Camerarius provided the impetus that boosted the casual interest in pollen to the level of fledgling science. He succeeded in unravelling the mystery of the fertilization mechanism in plants, thereby revealing at last the function of the curious yellow dust (Wodehouse, 1935).

The development of systematic palynology as a science, like many other fields, is closely allied to advancements in light microscopy. As optics improved, finer pollen characters were discernible, and their taxonomic value became increasingly evident. In 1830 John Lindley demonstrated the utility of pollen morphology in systematics when he used pollen characters as the basis for the establishment of 4 tribes of orchidaceous plants. By the mid-1830's both Julius Fritzsche and Hugo Von Mohl had constructed comprehensive classifications of pollen grain forms for large numbers of families (Wodehouse, 1935). And late in the 19th century Hugo Fischer conducted a critical examination of pollen from over 2000 species of 185 families. His studies contributed much to the body of knowledge about pollen grain formation and structure, and enabled him to demonstrate conclusively the enormous phylogenetic value of pollen grain characters (Wodehouse, 1935).

Wodehouse (1935) conducted the first modern study of Lactuceae pollen, examining pollen of 16 genera and 35 species. He described a beautiful sculpturing system composed of an interlocking network of high, spined ridges and lacunae, which he termed echinolophate. Echinolophate pollen, a distinguishing feature of many Lactuceae, also occurs in the tribes

Mutiseae and Vernonieae. Wodehouse also documented the presence of echinate (uniformly spiny) pollen in the tribe, and established the exomorphological terms in use today (Fig. 1).

Pollen morphology at the light microscope-level has been utilized in numerous modern systematic studies of the Lactuceae, including the tribal revision of Stebbins (1953), Saad (1961) and Boulos (1973) in the genus Sonchus, Davis and Raven (1962) in Malacothrix, and Northington (1971) in Pyrrhopappus. The use of modern tools such as SEM and TEM was less widespread until recently. Electron microscopy was employed by Northington (1974) in Pyrrhopappus, in an analysis of pollen endo- and exomorphology in a tribal overview by Tomb (1975) and in studies of the subtribes Stephanomeriinae and Microseridinae by Tomb, Larson and Skvarla (1974) and Feuer and Tomb (1977), respectively.

These various studies have shown the pollen grains of the Lactuceae to be highly sculptured and relatively undiversified in exomorphology. The grains are large (24-67 μm in equatorial diameter) and tricolporate. The exine structure is tectate-perforate and shape is open circular to subangular in polar view, and oblate-spheroidal in equatorial view. Most genera display echinolophate sculpturing but many belonging to the subtribe Stephanomeriinae have echinate pollen (Tomb et al., 1974).

The echinolophate Lactuceae are highly sculptured with sheer spined ridges arising abruptly from the lacunae. Lactuceae grains possess from 12-20 lacunae but 15 (3 poral, 6 abporal, 6 paraporal) is the most common number. Two systems of interlocking ridge networks circumscribe the lacunae. The equatorial ridge bisects the grain, separating the paraporal lacunae of one hemisphere from those of the other. The paraporal ridge system bounds the poral and abporal lacunae. The ridges are high and steep, jutting vertically outward from the grain proper. The spines borne

on the ridge are normally fused basally into the ridge with only the nonperforate tips visible. The grains are colporate, with large germinal apertures occupying most of the poral lacunae. A gap in the ridge which circumscribes the poral lacuna, the interlacunar gap, forms a canal connecting the poral and abporal lacunae. The gap is thought to facilitate harmomegathic movements (Wodehouse, 1935). The colpus expands through this gap and into the abporal lacunae. (See Figures 1 and 2 for diagrams of exo- and endomorphology, respectively.)

The polar thickening is a spiny plate which overlays the poles of the grain. This thickened plate may be narrow or broad, covering the entire pole and even extending into the mesocopal regions. Or it may be reduced so as to be merely the site of the confluence of the paraporal ridges that confine the abporal lacunae.

Spines are borne on the ridges, the poles, and occasionally are found to escape into the paraporal lacunae. Spines have globose (when free from the ridge) microperforate bases, and nonperforate apices. The tectum of the lacunae is also microperforate.

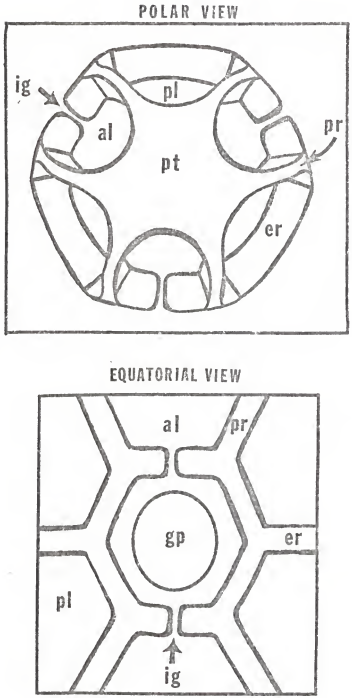
The diversity in endomorphology in the tribe is much greater than that of external sculpturing. The internal wall strata consists of 2 layers: the endexine and ektexine. The endexine is the inner layer and may consist of 1 or 2 distinct parts. The ektexine is comprised of 3 layers: a spiny tectum, columellae, and foot layer (Fig. 2). The foot layer caps the endexine and is separated from other elements of the ektexine by a small cavity, the cavus. Columellae are the rods which support the tectum. These rods are assembled into various numbers of levels and diverse configurations within the tribe. They may be solid or contain internal foramina; they may be small and anastomosing or massive and unbranched.

The details of Leontodontinae exo- and endomorphology are described in the Results section.

Figure 1. A diagram of the structures of Lactuceae echinolophate pollen grains, depicting the elaborate system of interlocking ridges and lacunae and the terms which describe these features.

FIGURE 1

LACTUCEAE POLLEN DIAGRAM



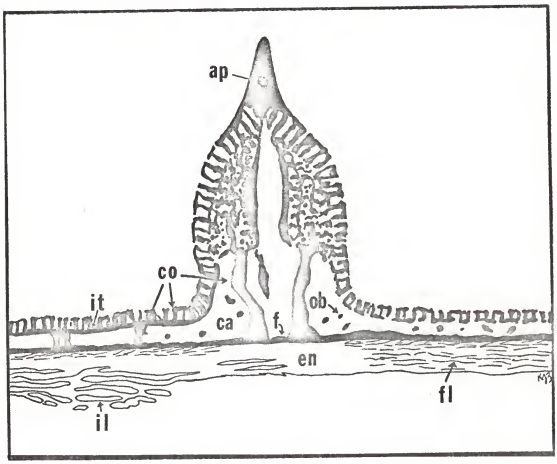
pt. Polar thickening
al. Abporal lacuna
pl. Paraporal lacuna
pr. Paraporal ridge
er. Equatorial ridge
ig. Interlacunar gap
gp. Germ pore within the poral lacuna

Diagrams & terminology from Wodehouse (1935)

Figure 2. A diagram of sectioned pollen exine, depicting the types of variations found in Leontodontinae pollen grains, and the terms which describe these variable endomorphic features.

FIGURE 2

LEONTODONTINAE ENDOMORPHOLOGY



en. Endexine

il. Indigenous lamellae

f. Foot layer

fl. Foot layer lamellations

ca. Cavus

ob. Oblique rods

it. Infratectum

co. Columellae

ap. Apical channel

MATERIALS AND METHODS

Unopened flower buds were removed from herbarium specimens of the Field Museum (F), The New York Botanical Garden (NY), the Gray Herbarium (GH), and the Smithsonian Institution (US). The source, locality and collection data are listed in Table 1. Forty-two species from 9 genera, a total of 64 specimens, were examined using LM and SEM. Representatives of each genus were examined in TEM. In selecting species for study, an attempt was made to obtain samples of each genus from its major centers of distribution. In Hypochoeris, species which had been objects of previous taxonomic studies were deliberately chosen in order to compare the earlier findings with the pollen data. Selection of species for study, especially in the small genera, was determined in part by access to and availability of herbarium material.

The floral tissue was softened in 10% potassium hydroxide for a minimum of 18 hours and then acetolyzed according to the Erdtman method (1960) as revised by Faegri and Iverson (1964). This technique is summarized as follows:

1. Softened florets with mature pollen were mashed on a ca 200 mesh copper screen to remove most flower parts, washed through the screen with 95% ethanol into a beaker, and transferred to a centrifuge tube.

2. Dehydration of this pollen mixture was accomplished by successive washings, first in 95% ethanol and then glacial acetic acid.

3. A 9:1 solution of acetic anhydride:sulfuric acid (conc.) was poured into each sample and all were placed into a boiling water bath for 10-20 minutes.

4. The samples were centrifuged hot for 2-3 minutes, after which the acetolysis mixture was decanted.

5. The samples were washed once in glacial acetic acid and 4 times in distilled water.

Acetolysis dissolves cellulose, pollen cytoplasm, intine (the wall layer directly under the exine), tapetal debris and proteins, lipids and

trace polysaccharides on the surface of the grain. Only the highly resistant sporopollenin of the outer pollen wall remains after acetolysis. Sporopollenin comprises the pollen exine but the exact nature of this substance is still under study, although it may well be a polymer of carotenoids and carotenoid esters (Brooks and Shaw, 1968; Shaw, 1971).

Post-acetolysis the samples were divided into fractions for LM, SEM, and TEM and stored in 70% ethanol.

For LM examination a small amount of glycerine jelly was placed on a glass slide and heated until it melted. Then a drop of the pollen-water mixture was mixed with the jelly, cover-slipped, and ringed with clear nail polish for permanence. Diameter in polar optical cross section for the equatorial diameter (E.D.), diameter in equatorial optical cross section for the polar diameter (P.D.), and spine length (S.L.) were measured for each grain using a Zeiss Universal microscope, with a 40X oil Planapo objective, at a magnification of 800X. (The procedure employed in obtaining measurements is diagrammed in Figure 3). Thirty grains from each specimen were measured for most taxa and calculations were made to determine mean, standard deviation (S.D.), and Polar/Equatorial diameter (P/E) ratio. Examination of sculpturing patterns and apertures were made with LM at magnifications of 800X and 1250X and with SEM.

Acetolyzed pollen residues for SEM were mounted in a drop of water on a circular cover slip that had been glued to an aluminum SEM stub with conductive silver paste. The samples were air-dried and then vapor-coated with ca 200-400 Å of gold-palladium alloy while rotating at a 45° angle with respect to the vapor source. Micrographs were made using an ETEC U-1 scanning electron microscope located in the Department of Entomology, Kansas State University.

For examination in TEM pollen residues were embedded in Spurr's Resin standard medium, modified for lower viscosity and long pot life (Spurr, 1969). Preparation was conducted as follows:

1. Acetolyzed samples that had been stored in 70% ethanol were further dehydrated in one wash of 95% ethanol and 2 washes of 100% ethanol, 10 minutes each.

2. Samples were infiltrated in a Spurr's Resin (SR) series: 3 ethanol:1 SR, 1 hour; 1 ethanol:1 SR, 1 hour; 100% fresh SR, minimum of 1 hour.

3. The majority of the resin was poured off and the pollen was transferred to a conical-tipped Beem capsule. New resin was added and the samples were centrifuged for 20-30 minutes at 3000 rpm or until the pollen was pelleted in the tip of the capsule.

4. The samples were left at room temperature for 2-4 hours before being cured (polymerization of the resin) at 70°C for 16-24 hours.

All samples were thin-sectioned with a DuPont diamond knife on a Reichert OM-2 Ultramicrotome. Approximately 75 nm - 120 nm sections (silver and gold reflection colors) were stained with 5% uranyl acetate in ethanol for 20-30 minutes followed immediately by staining with Reynolds lead citrate for 3-6 minutes. Micrographs were made using a Phillips 201 Electron microscope located in the Division of Biology, Kansas State University.

A set of the LM slides used in this study have been deposited in the Pollen and Spore Reference Collection at the University of Texas Herbarium (TEX) and at the Kansas State University Herbarium (KSC). A set of the TEM and SEM micrographs have also been placed on file at KSC.

Figure 3. A diagram illustrating the method used to measure 3 aspects of pollen size (equatorial diameter, polar diameter, spine length) in the light microscope.

FIGURE 3

METHOD OF MEASURING POLLEN IN LM

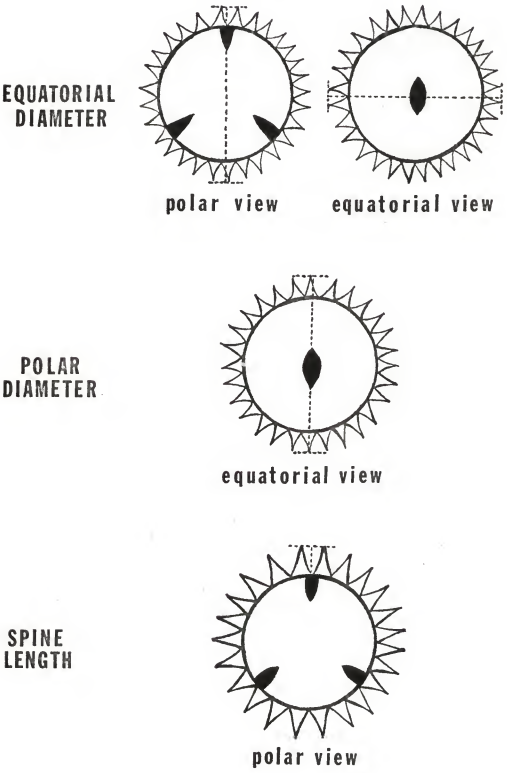


Table 1

COLLECTION DATA FOR SPECIMENS USED IN POLLEN STUDY

TAXON	SOURCE
Aposeris foetida (L.) Less.	Austria: Superioris. Neck s.n. (NY). Austria: Salzburg. Tscherning s.n. (F). Germany: Upper Bavaria, roadside bank near Garmisch. L.M. Andrews 856. (NY). Italy: Prov. di Belluno, San Vito del Cadore. (NY).
Garhadiolus hedypnois Jaub. et Spach	Israel: Jerusalem. Meyers 634. (F).
G. papposus Boiss. & Buhse	Africa: (NY).
Hedypnois cretica (L.) Dum.-Courset	Australia: 4 mi. west of Blanchetown. Willis 276. (F). Arizona: Tucson, Pima Co., lawn weed. R.B. Streets s.n. (NY). Texas: Corpus Christi. Benke 5451. (F).
H. polymorpha DC. (cretica (L.) Dum.-Courset, fidae Flora Europaea)	Corsica: Serra di Scopamene, par Sartene. E. Reverchon s.n. (NY).
H. monspeliensis Willd.	Morocco: Hab. in arenosis maritimis, pr. Andir. Dr. Font Quer s.n. (NY).
H. pendula DC.	Ex. Hb. Thleicher. Chanpenfier s.n. (NY).
Hyoseris lucida L. (radiata ssp. graeca Halacsy, fidae Flora Europaea)	Morocco: S.W. Tamir to Cape Ghir. P. & J. Davis 48450. (NY).
H. radiata ssp. radiata L.	France: lieux incultes du littoral à Ste. Hélène près Nice. Canut s.n. (NY). France: champs, lieux incultes, bords des chemins sur le calcaire à Nice (Alpes-Maritimis). S. Choulette s.n. (NY). France: Champs incultes à Nice. Bourgeau s.n. (F).
Hypochoeris acaulis (Remy) Britton	Bolivia: 50 km. S.E. of Cochambamba. Eyerdam 25059. (F).
H. achyrophorus L.	Africa: Tunisia, village of Korbous, in aridis incultis. C. J. Pitard s.n. (NY).

Table 1 (continued)

H. andina (DC.) Griesb. (arenaria v. andina (DC.) Cabrera, fidae Flora Patagonica)	Peru: Prov. Tayacaja, north of Pampas. Stork & Horton 10245. (F).
H. apargioides Hook. & Arn.	Peru: Dept. Cuzco, Prov. Canas, slopes of San Andreas de Checca. Vargas 11013. (F).
H. cretensis (L.) Bory & Chaub. in Bory	Greece: Euboea. K. H. Rechinger 16419. (US).
H. elata (Wedd.) Griesb.	Peru: Matucana. McBride & Featherstone 268. (F).
H. glabra L.	South Carolina: Camden, waste place. A. E. Radford 20767. (NY). Sweden: G. Samuelsson 1598. (NY).
H. grandiflora Ledeb.	China: Peitaiho, Hopei province. W. Y. Hsia 1833. (NY).
H. hohenackeri (Sch. Bip.) Domke	Ecuador: Imbabura, Lago San Marcos, Cayambe. P. C. D. Cazalet & T. D. Pennington 5425. (NY).
H. laevigata (L.) Cesati, Passer. & Gibelli	Morocco: 11 km. from Irherm to Taroudannt, rocky slopes. P. & J. Davis, D. 48894. (NY).
H. lutea Britton	Brazil: Paraná, Serra S'Ana (Balsa Nova). G. Hatschbach 22788. (NY).
H. microcephala var. microcephala (Sch. Bip.) Cabrera	Paraguay: Dept. of San Pedro. Wolston 592. (GH).
H. microcephala var. albiflora (O. Kuntze) Cabrera	Texas: 6 mi. N. of Orange, Orange Co. Shinners 31370. (GH).
H. radicata L.	New York: N. Y. City, Bedford Park. P. Nelson & K. D. Kimball s.n. (NY).
H. taraxacoides (Lois.) Benth. et. Hook.	Bolivia: LaPaz, pan Aoinos. Otto Buchtien s.n. (NY).
H. tenuifolia (Hook. & Arn.) Griesbach	Argentina: Pandel s.n. (NY).
H. tweediei (Hook. & Arn.) Cabrera	Florida: Holmes Co., 1.5 mi. N.E. of Westville, near Choctawatchee River. D. B. Ward 6465. (NY).

Table 1 (continued)

H. uniflora Vill.	Italy: Dolomite Mtns., (Val del Pan.). Werdermann & D. Meyer 168. (US).
H. variegata (Lam.) Baker en Martius	Argentina: Prov. Buenos Aires: Partido de Salvedra, Sierra de Cura-Malal. H. A. Fabris 4888. (NY).
L. asper (W. K.) Poir. (crispus spp. crispus Vill. fidae Flora Europaea)	Macedonia: in Monte Wodno. J. Bornmuller 1397. (NY).
L. asperrimus (Willd.) Boiss. ex Ball (crispus ssp. asperrimus (Willd.) Finch & P. D. Sell, fidae Flora Europaea)	Lebanon: G. Samuelsson s.n. (NY).
L. autumnalis L.	Labrador: Canada Mud Lake, Hamilton River. J. M. Gillett & Findlay, W. I. 5437. (US).
L. crispus (ssp. crispus Vill., fidae Flora Europaea)	Switzerland: Zermatten in Wallis. E. M. Thomas s.n. (NY).
L. hirsutus Hook.	Australia: near Adelaide. Kaspiew 814. (F).
L. hispanicus ssp. hispanicus (Willd.) Poiret (Picris hispanica (Willd.) P. D. Sell, fidae Flora Europaea)	Morocco: Near Titki between Tafraouten and Irherm. P. & J. Davis, D. 48815. (NY).
L. hispidus L.	France: Mouret, Jura Mts., Savoy. Ellys T. Moldenke 9041. (NY).
L. incanus (L.) Schrank	France: Corinth. Jeaupert 56. (F).
L. laciniatus (Bertol.) Widder	Iraq: near Bagdad. Lazar s.n. (F). Iraq: Ramadi Liwa Abu Ghranib. Barkley & Palmatier 1068. (F).
L. maroccanus (Pers.) Ball.	Morocco: 35 km. from Marrakech to Chichaoua. P. & J. Davis, D. 48207. (NY).
L. saxatilis spp. saxatilis Lam.	Azores: Pico, Candelaria near Porto de Ana Clara. P. Dansereau, A. R. Pinto Da Silva, B. V. Rainha 418. (NY).
Picris damascena v. homocarpa Eig. & Caill.	Syria: Antilibanon Mtns., Louk Ouadi Barada, solo calcareo, in rupestribus. G. Samuelsson s.n. (NY).

Table 1 (continued)

P. echioides L.	Australia: Adelaide. H. Eichler 14553. (NY). Italy: Modena. G. B. De Toni s.n. (NY).
P. hieracioides ssp. hieracioides	Pakistan: Karakoram Prov., Nagar Village. O. Polunin 6425. (F). Australia: Pt. Lonsdale, Victoria. Tilden 803. (F). Australia: New South Wales, Eucharlena. (NY). New Zealand: South Island. T. F. Chessman s.n. (NY). Russia: Prov. et. distr. Belgorod, prore pag. Toplinka, in declivitate montis apud marginem quercete. I. Pallon s.n. (NY).
P. hieracioides ssp. japonica (Thunb.) Krylv.	Japan: Honshu. Pref. Osaka near Kokubu, Kashiwara-shi. Gen. Murata 18600. (NY).
P. hieracioides ssp. kamtschatica (Ledeb.) Hult.	Alaska: Attu Island, Sarana Bay. Robert Hardy 285. (NY).
P. hieracioides ssp. squarrosus	Australia: Adelaide. Kaspiew 899. (F).
P. hieracioides ssp. villarsi (Jordan) Nyman	Sweden: Sk. Karpalund. (NY).
P. strigosa Bieb.	Palestine: Raurleh. Meyers & Dinsmore 3871. (F).
Rhagadiolus stellatus (L.) Gaertn.	Israel: Jerusalem, Mt. Scopus. Amdursky 199. (GH). Israel: Mt. Tabor. Meyers & Dinsmore 2340 b. (F).
Urospermum dalechampii (L.) Scop. ex. F. W. Schmidt	Corsica: Bastelica. Reverchon 143. (NY).
U. picroides (L.) Scop. ex. F. W. Schmidt	Iraq: near Bagdad. Lazar 504. (NY). France: Aix en Province. E. Jeaupert s.n. (F).

RESULTS

This section summarizes pollen morphological data obtained from representatives of 9 genera of the Lactuceae, the Leontodontinae subtribe (sensu Jeffrey). These data include LM measurements (summarized in Table 2), and descriptions of pollen shape and patterns of surface structure and sculpturing as revealed by LM and SEM. Endomorphological data derived from examination by TEM is also detailed for representative species. Exomorphology and endomorphology descriptions are presented in separate sections. Wodehouse's (1935) terminology is used to characterize exomorphology, while that of Faegri and Iverson (1964) is employed in descriptions of endomorphology and shape, as is the convention of most palynologists.

The detailed descriptions of exomorphologies are preceeded here by the following account of the kinds of variations encountered in the pollen characters and definitions of new terms. This format is also employed in the endomorphology section.

Exomorphology:

External sculpturing in the Leontodontinae (sensu Jeffrey) is almost exclusively echinolophate. Only certain species of Hypochoeris produce pollen that deviates far from this sculpturing system. Most taxa studied are tricolporate but several samples also contain percentages of tetracolporate grains. Shape in polar view is open circular, subangular or inter-hexagonal, and is oblate-spheroidal in equatorial view. Exine structure is tectate perforate.

Minor variations on the general theme occur in many features of sculpturing. The exomorphology of each species is described in terms of the variations in the following features: Grain shape; breadth and

topography of the polar thickening; shape and size of the abporal lacunae; size of the paraporal lacunae; character of the equatorial ridge (unilinear, bilinear, or disrupted); presence or absence of the polar-mesocopal ridge; grain measurements (P/E ratio, E.D., P.D., S.L.). Unless otherwise stated, all grains are echinolophate, tricolporate, and possess spines which are gradually tapered to a blunt apex.

Explanations of the types of variations found within certain features are expounded upon below for the sake of clarity and brevity in the pollen descriptions that follow. The new terms that are employed in the exomorphological descriptions are also explained.

1. Grain shape: Shape in polar view is given first followed by its appearance in equatorial view.

2. Polar thickening: The relative size of this spiny plate is described in terms of the approximate number of spines included therein, excluding those of the surrounding ridges. The region may be narrow in breadth, existing merely as the polar confluence of the ridge system (Figs. 4 and 10), or it may cover the entire surface area that is visible in the polar view (Figs. 36 and 38). Most species studied are intermediate between these two extremes. The presence of polar channels and/or polar lacunae also characterizes this region.

   a. Polar channels -- a characteristic of the polar thickening in which areas of sunken tectum circumscribe individual spines or clumps of several spines, thus appearing as channels or canals along the surface of the polar thickening (Fig. 48).

   b. Polar lacunae -- a feature present on the polar thickening of some species in which large circular-ovoid patches of spineless, sunken tectum appear as lacunae, one situated opposite each of the 3 paraporal lacunae (Figs. 7, 22, 43).

3. Paraporal lacunae: These lacunae occupy the mesocopal region (the area between pores, on either side of the equatorial ridge) and are described in the following terms:

a. Spines may encroach upon the paraporal lacunae from the pole, thus partially occluding the lacunae (Figs. 32, 34).

b. Fugitive spines are seemingly misplaced spines which occur, usually singly, within the paraporal lacunae. These spines are distinct from those which invade from the pole in that they normally occur singly and isolated from any other spines. The tendency toward production of these fugitive spines is characteristic of some species (Figs. 37, 49).

c. If neither of the above occur, the paraporal lacunae are termed vacant.

4. Equatorial ridge: This ridge which bisects the pollen grain is described in terms of the disposition of spines that are borne upon it. The ridge may be:

a. Unilinear -- refers to a ridge that bears a single row of spines which project radially from the grain proper. This type occurs most commonly.

b. Bilinear -- refers to a ridge that bears a double row of spines which project tangentially from the grain proper.

c. Disrupted -- this condition, which is intermediate between unilinear and bilinear, occurs in a ridge whose unilinearity is occassionally disrupted by a tangentially oriented offshoot spine (Fig. 53).

5. Polar-mesocopal ridge: The high, spiny ridge that borders the polar thickening in some species, giving definition to the boundary between the pole and the adjacent mesocopal region. When this ridge is ill-defined or absent, the limits of the polar thickening are also ill-defined, i.e., the spines of the polar thickening may invade the mesocopal region, partially occluding the paraporal lacunae. This polar-mesocopal dividing ridge may be well-defined (Fig. 17), somewhat fragmented (Fig. 32), or absent (Fig. 34).

The shape of the spines, the extent of basal fusion among spines of the ridges and polar thickening, and the number of spines per interporal segment of the equatorial ridge are also described if these are found to be unique or distinguishing features.

In the following exomorphological descriptions, the number of species studied per total number of species within the genus is indicated behind each genus heading. The number of specimens examined per species is noted behind each species heading.

Aposeris (1/1)

Aposeris foetida (4): Shape: open interhexagonal, spherical to oblate. Polar thickening: comprised of a unilinear tripartite ridge formed by the confluence of the 3 ridges which circumscribe the abporal lacunae. Abporal lacunae: large, oval to triangular, occupy much of the polar surface area. Paraporal lacunae: vacant, large because of expansion on to the pole. Equatorial ridge: unilinear, topped by tall, unusually stout spines. Polar-mesocopal ridge: well-defined. P/E ratio = 0.94, E.D. = 39.1 µm (± 1.3), P.D. = 36.7 µm (± 1.1), S.L. = 2.7 µm (± 0.16) (Figs. 6, 10).

Garhadiolus (2/5)

Garhadiolus hedypnois (1): Shape: open interhexagonal, spherical to oblate-compressed oval. Polar thickening: broad, with numerous (9-17) spines often basally fused to neighboring spines, forming small irregular ridges amid polar channels. Abporal lacunae: oval, much smaller than the poral lacunae. Paraporal lacunae: usually vacant, rarely contain fugitive spines. Equatorial ridge: unilinear. Polar-mesocopal ridge: well-defined. Tetracolporate grains accounted for ca 43% of the total grains in the sample. They differed from the tricolporate grains in size, pore number (4), lacunae number (20), smaller segments of equatorial ridge, and in their rectangular rather than triangular polar thickening. Tricolporate: P/E ratio = 0.92, E.D. = 37.4 µm (± 2.7), P.D. = 34.3 µm (± 2.3), S.L. = 2.2 µm (± 0.46). Tetracolporate: P/E ratio = 0.88, E.D. = 45.1 µm (± 1.7), P.D. = 39.5 µm (± 1.4), S.L. = 2.7 µm (± 0.27) (Figs. 19-21).

Garhadiolus papposus (1): Shape: open semi-angular, spherical-oblate. Polar thickening: broad, spines extend into the paraporal lacunae. Abporal lacunae: considerably smaller than previous species, oval. Paraporal lacunae: fugitive spines common. Equatorial ridge: unilinear. Paraporal ridge: indistinct or absent. P/E ratio = 0.90, E.D. = 30.9 µm (± 1.7), P.D. = 27.9 µm (± 1.5), S.L. = 1.6 µm (± 0.32).

Rhagadiolus (1/1)

Rhagadiolus stellatus (2): Shape: open interhexagonal, spherical-oblate. Polar thickening: consists only of the unilinear confluence of the ridges which circumscribe the abporal lacunae. Abporal lacunae: large, oval, occupies much of the polar surface area. Paraporal lacunae: vacant, large because of expansion onto the pole. Equatorial ridge: unilinear, spine bases partially free from adjacent spine bases. Polar-mesocopal ridge: well-defined. Spines do not occur apart from the ridge systems. P/E ratio = 0.92, E.D. = 33.5 µm (± 0.71), P.D. = 30.8 µm (± 0.10), S.L. = 2.2 µm (± 0.12) (Figs. 4, 5).

Hedypnois (3/4)

Representatives of this small genus were found to be echinolophate, open interhexagonal in polar view, and spherical to oblate in equatorial view. Variable morphological features are described below.

Hedypnois cretica (4): Approximately 44% of the grains examined were tetracolporate. Their shape in equatorial view is oblate-compressed oval, pore number is 4, lacunae number is 20. Otherwise, these grains are much like the tricolporate grains. Polar thickening: large, triangular, with 6-12 spines; rectangular with 17-25 spines in tetracolporate grains. Abporal lacunae: triangular. Paraporal lacunae: narrow, fugitive spines

occasional to common. Equatorial ridge: occasionally bilinear or disrupted. Spines are uniquely shaped in this species, having straight sides that taper sharply from a wide base to an acute peak, precisely cone-shaped. (One sample (Reverchon s.n.) possessed the usual gradually tapered blunt spines.) Polar-mesocopal ridge: well-defined, largely parallel to the equatorial ridge rather than sharply angled in the center, sometimes unattached to the polar thickening (Fig. 17). The detached polar thickening is an odd feature found to occur in ca 30% of the grains, both tri- and tetracolporate, in 3 of the 4 samples. The complete separation of the polar-mesocopal ridge from the polar thickening enables the 3 abporal lacunae to be fused laterally, thereby creating a lacunar moat around the polar thickening, and isolating it from the ridge systems (Fig. 16). In some grains this detachment is only partial. This sculpturing anomaly was not found in other species of Hedypnois or elsewhere in the subtribe. Tricolporate: P/E ratio = 0.90, E.D. = 34.8 µm (± 0.62), P.D. = 31.1 µm (± 1.0), S.L. = 2.1 µm (± 0.12). Tetracolporate: P/E ratio = 0.88, E.D. = 42.3 µm (± 1.2), P.D. = 37.2 µm (± 1.3), S.L. = 2.2 µm (± 0.1) (Figs. 8, 9, 13-17).

Hedypnois monspeliensis (1): Polar thickening: small, 4-12 spines. Abporal lacunae: large, circular. Paraporal lacunae: commonly vacant, fugitive spines rare. Equatorial ridge: unilinear. Polar-mesocopal ridge: well-defined. P/E ratio = 0.90, E.D. = 37.5 µm (± 1.7), P.D. = 33.5 µm (± 1.1), S.L. = 2.5 µm (± 0.19) (Fig. 18).

Hedypnois pendula (1): Polar thickening: narrow, 1-5 spines. Abporal lacunae: large, oval to triangular. Paraporal lacunae: commonly vacant, fugitive spines rare. Equatorial ridge: unilinear, globose spine bases are partially free of adjacent spine base. Polar-mesocopal ridge:

Figure 4. SEM micrograph of a pollen grain of Rhagadiolus stellatus, polar view, Meyers & Dinsmore 2340b (F). Note the polar thickening is reduced to a tripartite ridge. Line equals 10 µm.

Figure 5. SEM micrograph of a pollen grain of R. stellatus, equatorial view, Meyers & Dinsmore 2340b (F). Line equals 10 µm.

Figure 6. SEM micrograph of a pollen grain of Aposeris foetida, equatorial view, Italy (NY). Note the unusually stout spines. Line equals 10 µm.

Figure 7. SEM micrograph of a pollen grain of Hyoseris radiata ssp. radiata, polar view, Choulette s.n. (NY). Note the 3 polar lacunae. Line equals 10 µm.

Figure 8. SEM micrograph of a pollen grain of Hedypnois cretica, polar view, Benke 5451 (F). Note the peaked spines. Line equals 10 µm.

Figure 9. SEM micrograph of a pollen grain of H. cretica, equatorial view, Benke 5451 (F). Line equals 10 µm.

Figure 10. SEM micrograph of a pollen grain of Aposeris foetida, polar view, Italy (NY). Note the polar thickening is reduced to a tripartite ridge. Line equals 10 µm.

Figure 11. SEM micrograph of a pollen grain of Hyoseris radiata ssp. radiata, equatorial view, Bourgeau s.n. (F). Line equals 10 µm.

Figure 12. SEM micrograph of a pollen grain of Hyoseris radiata ssp. radiata, polar view, arrow indicates the polar lacuna, Choulette s.n. (NY). Line equals 1 µm.

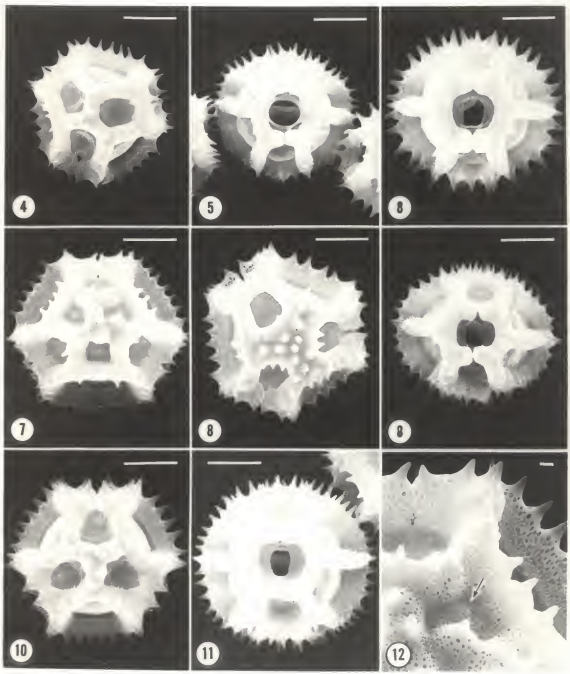

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Figure 13. SEM micrograph of a pollen grain of Hedypnois cretica, polar view, Willis 276 (F). Note peaked spines and triangular abporal lacunae.

Figure 14. SEM micrograph of pollen grains of H. cretica, depicting grain abnormalities and variability in size between tricolporate and tetracolporate grains, R. B. Streets s.n. (NY).

Figure 15. SEM micrograph of a tetracolporate pollen grain of H. cretica, polar view, Willis 276 (F).

Figure 16. SEM micrograph of a tricolporate pollen grain of H. cretica with a partially isolated polar thickening and connected abporal lacunae, polar view, Willis 276 (F).

Figure 17. SEM micrograph of a pollen grain of H. cretica, mesocopal view, showing small paraporal lacunae separated from the polar thickening by the polar mesocopal ridge (arrow). Willis 276 (F).

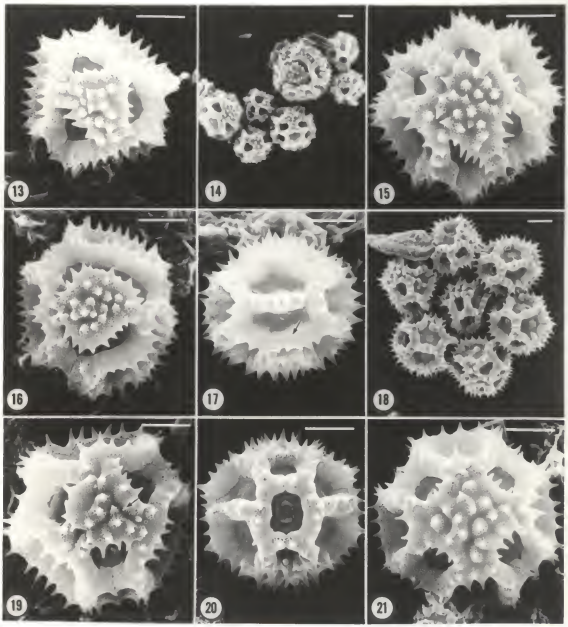
Figure 18. SEM micrograph of pollen grains of H. monspeliensis, Uriaguel s.n. (NY).

Figure 19. SEM micrograph of a pollen grain of Garhadiolus hedypnois, polar view, Meyers 634 (F). Arrow indicates polar channels.

Figure 20. SEM micrograph of a pollen grain of G. hedypnois, equatorial view, Meyers 634 (F).

Figure 21. SEM micrograph of a tetracolporate pollen grain of G. hedypnois, polar view, Meyers 634 (F). Note polar channels.

Line equals 10 μm.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well-defined. P/E ratio = 0.93, E.D. = 40.3 μm (± 1.5), P.D. = 37.5 μm (± 1.8), S.L. = 2.3 μm (± 0.43).

Hyoseris (1/3)

Two subspecies of Hyoseris, a small Mediterranean genus, are examined here. They are identical in most features but diverge slightly in the topography of the polar thickening as described below.

Hyoseris radiata (4): Shape: open interhexagonal, spherical-oblate. Abporal lacunae: large, oval to circular. Paraporal lacunae: large, vacant. Equatorial ridge: unilinear, spine bases sometimes not entirely fused to adjacent spines. Polar-mesocopal ridge: well-defined. (Figs. 7, 11, 12).

ssp. radiata (3): Polar thickening: bears 3 polar lacunae separated by 4-9 centrally located, basally fused spines. P/E ratio = 0.93, E.D. = 38.8 μm (± 0.83), P.D. = 36.0 μm (± 0.55), S.L. = 2.2 μm (± 0.12) (Fig. 7).

ssp. graeca (1): Polar thickening: large, with 9-12 spines and a tendency toward polar channels among the spines rather than polar lacunae. P/E ratio = 0.91, E.D. = 39.8 μm (± 2.3), P.D. = 36.2 μm (± 1.6), S.L. = 2.4 μm (± 0.20).

Hypochoeris (19/100)

Hypochoeris is a cosmopolitan genus of ca 100 species with main centers of distribution in South America, Eurasia, and the Mediterranean region. Exomorphologically it is the most eurypalynous genus of the Leontodontinae. Sculpturing patterns vary from echinolophate to nearly echinate. Shapes range from open circular to interhexagonal in polar view, and spherical to oblate in equatorial view.

Distinctions in pollen morphology correspond roughly to the several geographic centers of the genus. This being the case, the descriptions are assembled into three categories based on geographic distribution of the taxa.

I. Central Europe - Asia

The pollen of this assembly of species is distinguished primarily by its extremely large size. Sculpture: echinolophate. Shape: open interhexagonal, spherical to oblate.

Hypochoeris grandiflora (1): Polar thickening: small, 0-6 spines, the central patch of tectum between the surrounding ridges is often depressed and devoid of spines. Abporal lacunae: large, oval-triangular. Paraporal lacunae: large, fugitive spines rare. Equatorial ridge: exceptionally high, unilinear, spines bases partially free from the ridge. Polar-mesocopal ridge: well-defined. P/E ratio = 0.92, E.D. = 58.2 µm (± 3.9), P.D. = 53.3 µm (± 3.0), S.L. = 4.0 µm (± 0.49) (Figs. 29, 30).

Hypochoeris uniflora (1): Polar thickening: large, 2-11 spines. Abporal lacunae: large, oval-triangular. Paraporal lacunae: fugitive spines are rare but spines often encroach from the pole. Equatorial ridge: unilinear, spine bases may be only partially fused to the ridge. Polar-mesocopal ridge: indistinct. P/E ratio = 0.91, E.D. = 46.9 µm (± 2.0), P.D. = 42.8 µm (± 2.1), S.L. = 3.1 µm (± 0.45) (Figs. 26, 27).

II. Mediterranean - North Africa

The pollen of this assembly of species is among the smallest in the genus. The pollen grains hold the following morphological features in

common. Sculpture: echinolophate. Shape: open interhexagonal. Polar thickening: small, often bearing as few as 2 spines. Abporal lacunae: triangular to oval. Paraporal lacunae: large, vacant. Equatorial ridge: unilinear row of short spines. Polar-mesocopal ridge: well-defined. Details of polar sculpturing and other variable characters are described below.

Hypochoeris achyrophorus (1): Polar thickening: 2-9 spines, with prominent polar channels between spine clusters. P/E ratio = 0.91, E.D. = 30.9 µm (± 1.7), P.D. = 28.3 µm (± 1.6), S.L. = 1.9 µm (± 0.35).

Hypochoeris laevigata (1): Polar thickening: 3-7 spines with polar channels between the individual spines. P/E ratio = 0.91, E.D. = 30.7 µm (± 1.4), P.D. = 27.9 µm (± 1.3), S.L. = 1.1 µm (± 0.32).

Hypochoeris cretensis (1): Polar thickening: commonly spineless (0-2 spines) within the ridge system that bounds the polar thickening. Equatorial ridge: spines are elongate and globose spine bases are sometimes partially free from the ridge. P/E ratio = 0.91, E.D. = 35.1 µm (± 1.4), P.D. = 31.8 µm (± 0.71), S.L. = 2.2 µm (± 0.30) (Fig. 28).

The two species described below exist on many continents today as international weeds. Their pollen morphology is similar to that of the Mediterranean group in size as well as in the following characters. Sculpture: echinolophate. Shape: interhexagonal, spherical to oblate. Abporal lacunae: triangular to oval. Paraporal lacunae: usually vacant, fugitive spines rare. Equatorial ridge: unilinear row of low

spines, spines bases not entirely fused into the ridge. Polar-mesocopal ridge: well-defined.

Hypochoeris glabra (2): Polar thickening: 0-5 spines, spine bases may be fused or free, with polar channels between spines. Variation in the amount of polar channelling was considerable between the two specimens examined. P/E ratio = 0.93, E.D. = 29.5 µm (± 0.74), P.D. = 27.4 µm (± 0.69), S.L. = 1.6 µm (± 0.22) (Figs. 23, 24).

Hypochoeris radicata (1): Polar thickening: contains 3 polar lacunae circumscribed by spined ridges. P/E ratio = 0.95, E.D. = 31.6 µm (± 2.5), P.D. = 30.1 µm (± 1.1), S.L. = 1.8 µm (± 0.32) (Fig. 22).

III. South American

Hypochoeris in South America is widely diverse in pollen morphology, ranging from echinolophate to nearly echinate. Therefore, this category is further divided into 3 groups: echinolophate, modified echinolophate, and subechinate. The 3 groups comprise a continuum of variation primarily in the degree of occlusion of the paraporal lacunae and the fragmentation or disruption of the ridge system.

A. Echinolophate species

Shape: open semiangular to interhexagonal, spherical to oblate. Polar thickening: moderately large, densely spiny, spines extend into the mesocopal region. Abporal lacunae: large, triangular to oval. Paraporal lacunae: partially obscured by occasional fugitive spines, spined extension of the polar thickening, and equatorial ridge offshoot spines. Equatorial ridge: unilinear or frequently disrupted, spine tips elongate, bases sometimes not entirely fused to the adjacent spine bases. Polar-mesocopal ridge: indistinct or absent.

Hypochoeris tenuifolia (1): Polar thickening: spine bases partially free from the tectum. P/E ratio = 0.89, E.D. = 42.4 μm (± 2.1), P.D. = 37.7 μm (± 1.2), S.L. = 2.9 μm (± 0.43) (Figs. 31, 32).

Hypochoeris variegata (1): Polar thickening: spines partially obscure abporal lacunae in the polar view, spine bases are partially free. P/E ratio = 0.95, E.D. = 38.3 μm (± 2.2), P.D. = 36.5 μm (± 1.7), S.L. = 2.8 μm (± 0.35).

Hypochoeris lutea (1): Polar thickening: contains polar channels amid groups of spines fused at the base to create small ridges. P.E ratio = 0.94, E.D. = 36.6 μm (± 2.0), P.D. = 34.5 μm (± 1.9), S.L. = 2.9 μm (± 0.52).

B. Modified echinolophate species

These grains occupy approximate midpoint on the continuum of variation between echinolophate and subechinate. Because of the extensive polar thickening and small abporal lacunae the grains often appear subechinate in polar view. However, the equatorial ridge system is quite distinct. The paraporal lacunae are obscured to a greater degree than in the previous group due to fugitives and to invasion of spines from the polar thickening. Shape: open circular to semiangular, spherical to oblate. Polar thickening: covers the entire surface area of the pole, densely spiny. Abporal lacunae: nearly hidden in polar view by spines of the polar thickening, diminutive, much smaller than poral lacunae. Paraporal lacunae: diminished in size by fugitives and encroachment of spines from the polar thickening. Equatorial ridge: commonly unilinear, occasionally bilinear, all spine tips are exceptionally elongate, spine bases not entirely fused to adjacent spine bases. Polar-mesocopal ridge: absent.

Hypochoeris apargioides (1): Globose spines bases are evident atop the ridges. Bilinear equatorial ridges are common. P/E ratio = 0.86, E.D. = 35.8 µm (± 1.7), P.D. = 30.7 µm (± 1.4), S.L. = 2.7 µm (± 0.48).

Hypochoeris arenaria subsp. spathulata (1): The globose bases of the spines of the polar thickening are evident amid the polar channels. Spines are sometimes basally fused to adjacent spines. P/E ratio = 0.88, E.D. = 41.9 µm (± 2.9), P.D. = 37.0 µm (± 2.0), S.L. = 3.7 µm (± 0.39) (Fig. 35).

Hypochoeris hohenackeri (1): An exceptionally wide interlacunar gap is created by the absence of the ridge process that normally projects into the poral region and separates the poral and abporal lacunae. The aperture and poral lacunae are quite large relative to the abporal lacunae. P/E ratio = 0.95, E.D. = 43.1 µm (± 1.8), P.D. = 40.8 µm (± 1.5), S.L. = 3.8 µm (± 0.60) (Figs. 33, 34).

C. Subechinate species

The pollen of these species approach the echinate mode of surface sculpturing closely. The grains initially appear echinate but upon closer scrutiny, ill-defined ridges and occluded lacunae can be seen. Shape: open circular to semiangular, spherical to oblate. Polar thickening: large, covering nearly the entire surface area visible in polar view, densely spiny, spines extend far into the paraporal lacunae. Abporal lacunae: small, often obscured in polar view by spines of the polar thickening. Paraporal lacunae: nearly obliterated by fugitive spines and those spines encroaching from the polar region. Equatorial ridge: sometimes unilinear but often broken into ridge fragments due

to the incomplete fusion of adjacent spine bases, may also be bilinear or frequently disrupted. Polar-mesocopal ridge: absent.

Hypochoeris microcephala v. microcephala (1): Equatorial ridges are often bilinear but distinct, lacunae are partially obscured by spines but still well-defined. P/E ratio = 0.91, E.D. = 38.2 µm (± 2.1), P.D. = 34.8 µm (± 1.8), S.L. = 2.6 µm (± 0.39).

Hypochoeris microcephala v. albiflora (1): Equatorial ridge a low, bilinear ridge of partially fused spines, lacunae obscure. P/E ratio = 0.92, E.D. = 36.2 µm (± 2.5), P.D. = 33.2 µm (± 2.1), S.L. = 2.9 µm (± 0.43).

Hypochoeris acaulis (1): Sample is comprised of ca 50% tetracolporate grains. Polar spines are inclined to form short ridges by basal fusion. The equatorial ridge is often bilinear; ridges and lacunae are distinct. Tricolporate: P/E ratio = 0.89, E.D. = 41.6 µm (± 2.4), P.D. = 37.0 µm (± 1.6), S.L. = 3.1 µm (± 0.48). Tetracolporate: P/E ratio = 0.86, E.D. = 46.9 µm (± 4.8), P.D. = 40.2 µm (± 3.4), S.L. = 3.0 µm (± 0.62).

Hypochoeris tweediei (1): Sample is comprised of ca 27% tetracolporate grains. Equatorial ridge is unilinear but appears fragmented, spine bases are only partially fused; distinct lacunae; exceptionally wide interlacunar gaps. Tricolporate: P/E ratio = 0.90, E.D. = 34.4 µm (± 1.8), P.D. = 30.9 µm (± 1.8), S.L. = 2.5 µm (± 0.41). Tetracolporate: P/E ratio = 0.92, E.D. = 35.6 µm (± 2.1), P.D. = 32.9 µm (± 2.3), S.L. = 2.2 µm (± 0.33) (Figs. 36, 37).

Figure 22. SEM micrograph of a pollen grain of Hypochoeris radicata, polar view, Nelson & Kimball s.n. (NY). Arrow indicates polar lacunae. Note the remnant of a colpus in the lower left abporal lacunae.

Figure 23. SEM micrograph of a pollen grain of H. glabra, polar view, Samuelsson 1598 (NY).

Figure 24. SEM micrograph of a pollen grain of H. glabra, equatorial view, Samuelsson 1598 (NY).

Figure 25. SEM micrograph of a pollen grain of H. achyrophorous, polar view, Pitard s.n. (NY). Arrow indicates polar channels.

Figure 26. SEM micrograph of a pollen grain of H. uniflora, equatorial view, Werdermann & Meyer 168 (US).

Figure 27. SEM micrograph of a pollen grain of H. uniflora, polar view, Werdermann & Meyer 168 (US).

Figure 28. SEM micrograph of a pollen grain of H. cretensis, polar view, Rechinger 16419 (US). Note the small, nearly spineless, polar thickening.

Figure 29. SEM micrograph of a pollen grain of H. grandiflora, equatorial view, Hsia 1833 (NY). Note the extremely high ridges.

Figure 30. SEM micrograph of a pollen grain of H. grandiflora, polar view, Hsia 1833 (NY). Note the small, nearly spineless, polar thickening.

Line equals 10 μm.

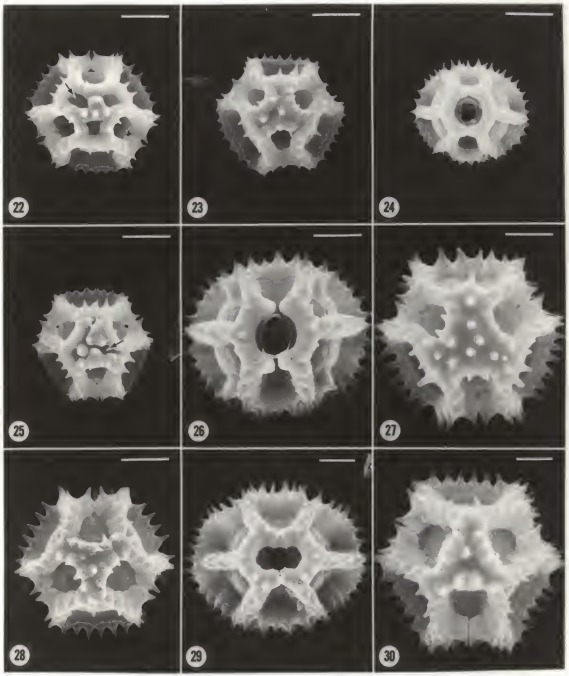
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Figure 31. SEM micrograph of a pollen grain of Hypochoeris tenuifolia, polar view, Pandel s.n. (NY).

Figure 32. SEM micrograph of a pollen grain of H. tenuifolia, equatorial view, Pandel s.n. (NY). Arrow indicates spines invading the paraporal lacunae from the pole in the absence of a distinct polar mesocopal ridge.

Figure 33. SEM micrograph of a pollen grain of H. hohenackeri, modified echinolophate, polar view, Cazalet & Pennington 5425 (NY).

Figure 34. SEM micrograph of a pollen grain of H. hohenackeri, equatorial view, showing small paraporal lacunae and encroaching spines. Note the large interlacunar gaps. Cazalet & Pennington 5425 (NY).

Figure 35. SEM micrograph of a pollen grain of H. arenaria v. andina, modified echinolophate, polar view, Stork & Horton 10245 (F).

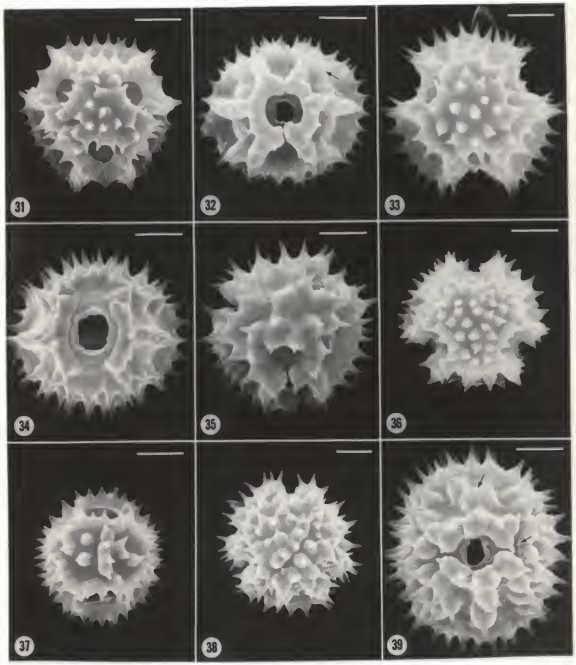
Figure 36. SEM micrograph of a pollen grain of H. tweediei, subechinate, polar view, Ward 6465 (NY). Note the extensive polar thickening.

Figure 37. SEM micrograph of a pollen grain of H. tweediei, mesocopal view showing fugitive spines within the paraporal lacunae, Ward 6465 (NY).

Figure 38. SEM micrograph of a pollen grain of H. taraxacoides, subechinate, polar view, Buchtien s.n. (NY).

Figure 39. SEM micrograph of a pollen grain of H. taraxacoides, equatorial view, showing fragmented equatorial ridge (arrow), small abporal lacunae (arrow), and the nearly occluded paraporal lacunae, Buchtien s.n. (NY).

Line equals 10 μm.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Hypochoeris elata (1): Equatorial ridge is bilinear, lacunae are largely obscure. P/E ratio = 0.88, E.D. = 36.3 µm (± 1.4), P.D. = 31.9 µm (± 1.4), S.L. = 2.5 µm (± 0.26).

Hypochoeris taraxacoides (1): This species approaches the echinate mode of sculpturing most closely; only the subtlest hints of ridges and lacunae prevent the pollen of this species from being termed echinate. There is only weak fusion between the spines that comprise the fragmentary equatorial ridge. All lacunae except the poral lacunae are nearly obliterated by spines. Spines are extremely elongate, the tallest observed in the subtribe, and are inclined toward basal fusion with neighboring spines to create short ridges. P/E ratio = 0.96, E.D. = 45.0 µm (± 2.2), P.D. = 43.4 µm (± 2.2), S.L. = 4.3 µm (± 0.71) (Figs. 38, 39).

Leontodon (8/50)

Leontodon is a large, essentially stenopalynous genus. Sculpturing pattern is echinolophate, shape is open interhexagonal in polar view, spherical to oblate in equatorial view. Although the pollen grains of the samples examined are fairly homogeneous in form, variations in patterns of exine sculpturing make it convenient to divide the species into 2 groups based on pollen exomorphology. Distinguishable tendencies mark the boundary between the groups. Variation among individual grains of a species is considerable and this variation occasionally obscures this artificial boundary between the pollen groups.

Hirsutus Group

Polar thickening: small, bears fewer than 10 spines, propensity toward polar channels and/or polar lacunae. One polar lacuna is adjacent

to each of the 3 paraporal lacunae and a central spiny area lies between them. The integrity of these polar lacunae is variable among the species, and sometimes between the individuals of one specimen. Abporal lacunae: large, oval to triangular in polar view. Paraporal lacunae: vacant, fugitive spines rare. Equatorial ridge: high, unilinear, rarely disrupted. Polar-mesocopal ridge: well-defined.

Leontodon hirsutus (1): Polar thickening has the maximum development of polar lacunae, but polar channels are also evident in the spiny central area. P/E ratio = 0.86, E.D. - 39.2 µm (± 1.7), P.D. = 33.6 µm (± 1.6), S.L. = 2.4 µm (± 0.41) (Fig. 43).

Leontodon saxatilis (1): Occasional tendency toward polar lacunae, but polar channelling is always distinct. P/E ratio = 0.89, E.D. = 36.4 µm (± 1.1), P.D. = 32.2 µm (± 0.90), S.L. = 2.0 µm (± 0.41) (Figs. 47, 48).

Leontodon maroccanus (1): Variation within the sample in sculpturing of the polar thickening ranges from the presence of distinct polar lacunae, to less distinct lacunae that are partially obscured by intruding spines, to only a subtle hint of polar channelling. Polar channels are often present in the spiny area between the 3 polar lacunae. P/E ratio = 0.90, E.D. = 36.7 µm (± 1.2), P.D. = 33.0 µm (± 1.0), S.L. = 1.8 µm (± 0.26) (Fig. 46).

Leontodon autumnalis (1): Polar channels are evident; polar lacunae are absent. P/E ratio = 0.93, E.D. = 38.6 µm (± 2.3), P.D. = 36.1 µm (± 1.4), S.L. = 2.8 µm (± 0.47).

Leontodon laciniatus (2): Polar channels are evident; polar lacunae are absent; abporal lacunae are unusually small and round. P/E ratio = 0.90, E.D. = 34.1 µm (± 1.2), P.D. = 30.8 µm (± 0.35), S.L. = 2.1 µm (± 0.01) (Figs. 41, 42).

Crispus Group

These grains are somewhat larger (E.D. = 37-41 µm) than those of the Hirsutus Group (E.D. = 34-39 µm) and differ slightly in sculpturing of the polar thickening and integrity of the paraporal lacunae. Polar thickening: varies from small to large, bears 5-30 spines, no tendency toward polar lacunae but polar channels do occur amid the spines. Abporal lacunae: large, triangular to oval. Paraporal lacunae: obscured by occasional to abundant fugitive spines or the encroachment of spines from the polar region. Equatorial ridge: high, unilinear, occasionally disrupted. Polar-mesocopal ridge: indistinct.

Leontodon hispidus (1): Polar thickening: 6-9 spines. P/E ratio = 0.91, E.D. = 41.1 µm (± 2.4), P.D. = 37.2 µm (± 1.9), S.L. = 2.4 µm (± 0.34).

Leontodon crispus ssp. asperrimus (1): Polar thickening: large, bears 15-30 spines, spines extend deep into the mesocopal region, diminishing the size of the paraporal lacunae. Fugitive spines are occasional. P/E ratio = 0.88, E.D. = 39.8 µm (± 1.6), P.D. = 35.1 µm (± 1.4), S.L. = 2.5 µm (± 0.36) (Fig. 40).

Leontodon asper (1): Polar thickening: small, bears 8-12 spines. Paraporal lacunae: fugitive spines abundant. P/E ratio = 0.93, E.D. = 36.8 µm (± 1.6), P.D. = 34.1 µm (± 1.6), S.L. = 2.4 µm (± 0.34) (Fig. 44).

Figure 40. SEM micrograph of a pollen grain of Leontodon crispus ssp. asperrimus, polar view, Samuelsson s.n. (NY).

Figure 41. SEM micrograph of a pollen grain of L. laciniatus, equatorial view, Lazar s.n. (F). Arrow indicates the distinct polar mesocopal ridge.

Figure 42. SEM micrograph of a pollen grain of L. laciniatus, polar view, Parkley & Palmatier 1068 (F). Arrow indicates polar channels. Note the small, circular abporal lacunae.

Figure 43. SEM micrograph of a pollen grain of L. hirsutus, polar view showing polar lacunae and polar channels, Kaspiew 814 (F).

Figure 44. SEM micrograph of a pollen grain of L. asper, equatorial view, showing abundant fugitive spines, Bornmuller 1397 (NY).

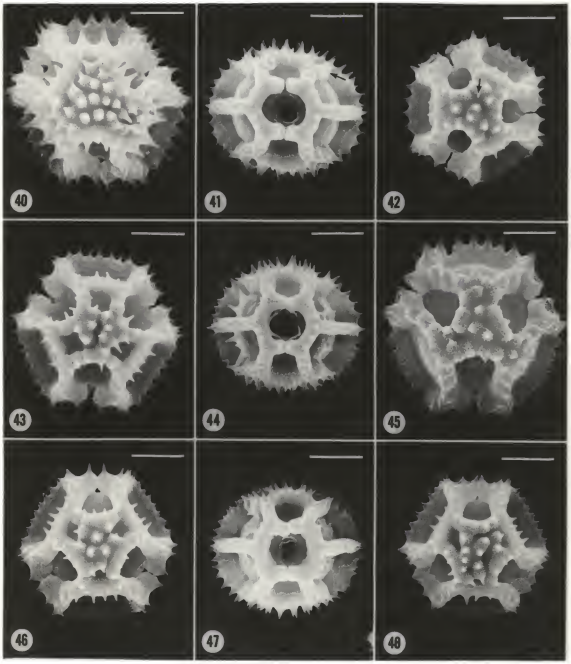
Figure 45. SEM micrograph of a pollen grain of L. crispus ssp. crispus, polar view, Thomas s.n. (NY).

Figure 46. SEM micrograph of a pollen grain of L. maroccanus, polar view, showing polar lacunae and polar channels, P. & J. Davis D. 48207 (NY).

Figure 47. SEM micrograph of a pollen grain of L. saxatilis ssp. saxatilis, equatorial view, Dansereau, Pinto Da Silva, & Rainha 418 (NY).

Figure 48. SEM micrograph of a pollen grain of L. saxatilis ssp. saxatilis, polar view showing polar channels, Dansereau, Pinto Da Silva, & Rainha 418 (NY).

Line equals 10 μm.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Leontodon crispus ssp. crispus (1): Polar thickening: small, bears 5-10 spines, polar channels are rare. Paraporal lacunae: occasional fugitive spines. P/E ratio = 0.92, E.D. = 37.2 µm (± 1.5), P.D. = 34.4 µm (± 1.2), S.L. = 2.1 µm (± 0.35) (Fig. 45).

Leontodon incanus (1): Polar thickening: small, bears 7-13 spines. P/E ratio = 0.86, E.D. = 41.3 µm (± 3.3), P.D. = 35.7 µm (± 2.2), S.L. = 2.7 µm (± 0.36).

Picris (6/40-50)

The species of Picris examined within the confines of this investigation are essentially stenopalynous. However, this genus was found to be useful in illustrating intraspecific, infraspecific, and geographic variation; in other words, the instability of the subtle variations in pollen exomorphology. Picris hieracioides is used here as the vehicle for studying variation and so is described separately from the other members of the genus.

Picris hieracioides (9): Shape: open interhexagonal, spherical-oblate. Polar thickening: variable in spininess. Abporal lacunae: large, oval to triangular in polar view. Paraporal lacunae: fugitive spines may occur singly, in groups, or not at all, but spines normally encroach from the polar region. Equatorial ridge: largely unilinear, frequently disrupted, occasionally bilinear, with 3-8 spines per interporal segment. Polar-mesocopal ridge: ill-defined or absent.

ssp. hieracioides (Russia): Polar thickening: 4-9 spines, distinct polar channels. Paraporal lacunae: fugitive spines absent. Equatorial ridge: unilinear, 6-8 spines per interporal

segment. P/E ratio = 0.87, E.D. = 44.7 µm (± 2.5), P.D. = 39.0 µm (± 1.5), S.L. = 2.8 µm (± 0.39) (Fig. 54).

ssp. hieracioides (Pakistan): Polar thickening: 7-14 spines. Paraporal lacunae: occasional fugitive spines. Equatorial ridge: unilinear, occasionally bilinear, 5-7 spines per interporal segment. P/E ratio = 0.88, E.D. = 41.0 µm (± 2.0), P.D. = 36.0 µm (± 1.4), S.L. = 2.8 µm (± 0.40).

ssp. hieracioides (New South Wales): Polar thickening: 5-12 spines. Paraporal lacunae: polar spines occlude much of the lacunae, fugitive spines common. Equatorial ridge: unilinear, frequently disrupted, 5-7 spines per interporal segment. P/E ratio = 0.92, E.D. = 41.5 µm (± 2.4), P.D. = 38.1 µm (± 1.3), S.L. = 2.7 µm (± 0.27) (Fig. 53).

ssp. hieracioides (Australia): Polar thickening: 6-12 spines. Paraporal lacunae: fugitive spines common. Equatorial ridge: unilinear, occasionally disrupted, 4-6 spines per interporal segment. P/E ratio = 0.87, E.D. = 41.1 µm (± 1.6), P.D. = 35.9 µm (± 1.5), S.L. = 2.5 µm (± 0.44) (Figs. 49, 50, 51).

ssp. hieracioides (New Zealand): Polar thickening: 12-17 spines. Paraporal lacunae: fugitive spines rare. Equatorial ridge: unilinear, 6-8 spines per interporal segment. P/E ratio = 0.91, E.D. = 38.4 µm (± 1.6), P.D. = 34.9 µm (± 1.1), S.L. = 2.3 µm (± 0.30).

ssp. japonica (Japan): Polar thickening: 4-10 spines. Paraporal lacunae: fugitive spines rare. Equatorial ridge: unilinear, 3-7

spines per interporal segment. Polar-mesocopal ridge: unusually distinct between the pole and mesocopal region, limiting polar spines to the pole. P/E ratio = 0.90, E.D. = 37.0 µm (± 1.7), P.D. = 33.1 µm (± 1.4), S.L. = 2.5 µm (± 0.31).

ssp. kamtschatica (Alaska): Polar thickening: 3-8 spines. Paraporal lacunae: fugitive spines occasional, polar spines often extend far into the mesocopal region. Equatorial ridge: Unilinear, occasionally disrupted, 3-7 spines per interporal segment. P/E ratio = 0.92, E.D. = 38.2 µm (± 1.8), P.D. = 35.0 µm (± 1.7), S.L. = 2.8 µm (± 0.43) (Fig. 52).

ssp. squarrosus (Australia): Polar thickening: 7-12 spines. Paraporal lacunae: fugitive spines common. Equatorial ridge: unilinear, 4-6 spines per interporal segment. P/E ratio = 0.87, E.D. = 42.4 µm (± 1.4), P.D. = 37.0 µm (± 1.6), S.L. = 2.6 µm (± 0.29).

ssp. villarsi (Sweden): Polar thickening: 4-8 spines amid polar channels. Paraporal lacunae: vacant. Equatorial ridge: unilinear, 5-7 spines per interporal segment. P/E ratio = 0.90, E.D. = 38.3 µm (± 1.1), P.D. = 34.4 µm (± 0.77), S.L. = 2.5 µm (± 0.35).

The remaining species of Picris examined here are a relatively homogeneous assemblage with respect to most exomorphological sculpturing features. Shape: open interhexagonal, spherical-oblate. Polar thickening: variously spiny, spines confined to the pole, never reaching into the mesocopal region. Abporal lacunae: large, oval to triangular. Paraporal lacunae: usually vacant, fugitive spines are

Figure 49. SEM micrograph of a pollen grain of Picris hieracioides ssp. hieracioides, polar view, Tilden 803 (F). Arrow indicates fugitive spine.

Figure 50. SEM micrograph of a pollen grain of P. hieracioides ssp. hieracioides, polar view, Tilden 803 (F).

Figure 51. SEM micrograph of a pollen grain of P. hieracioides ssp. hieracioides, equatorial view, Tilden 803 (F).

Figure 52. SEM micrograph of a pollen grain of P. hieracioides ssp. kamschatica, polar view, Hardy 285 (NY).

Figure 53. SEM micrograph of a pollen grain of P. hieracioides ssp. hieracioides, equatorial view showing spines encroaching upon the paraporal lacunae from the polar thickening, New South Wales (NY). Arrow indicates a disrupted equatorial ridge.

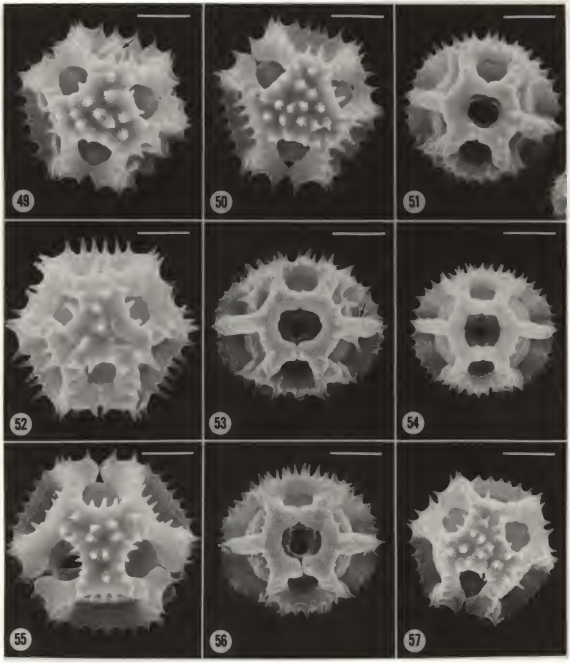
Figure 54. SEM micrograph of a pollen grain of P. hieracioides ssp. hieracioides, equatorial view, Pallon s.n. (NY).

Figure 55. SEM micrograph of a pollen grain of P. echioides, polar view, De Toni s.n. (NY). Note the remnant of a colpus in the lower left abporal lacuna.

Figure 56. SEM micrograph of a pollen grain of P. echioides, equatorial view, Eichler 14553 (NY).

Figure 57. SEM micrograph of a pollen grain of P. damascena v. homocarpa, polar view, Samuelsson s.n. (NY).

Line equals 10 μm.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rare. Equatorial ridge: unilinear, 5-9 spines per interporal segment. Polar-mesocopal ridge: well-defined.

Picris echioides (2): Polar thickening: 2-10 spines amid polar channels. Equatorial ridge: 5-7 spines per interporal segment. P/E ratio = 0.93, E.D. = 38.5 µm (± 2.3), P.D. = 35.8 µm (± 2.7), S.L. = 2.2 µm (± 0.16) (Figs. 55, 56).

Picris strigosa (1): Polar thickening, 7-9 spines amid polar channels. Equatorial ridge: 5-7 spines per interporal segment. P/E ratio = 0.87, E.D. = 39.5 µm (± 1.1), P.D. = 34.1 µm (± 1.1), S.L. = 2.3 µm (± 0.40).

Picris damascena v. homocarpa (1): Polar thickening: 3-12 spines amid polar channels. Equatorial ridge: 5-9 exceptionally short spines per interporal segment. Single spines occasionally invade the paraporal lacunae from the polar region. P/E ratio = 0.90, E.D. = 36.7 µm (± 1.6), P.D. = 32.9 µm (± 1.1), S.L. = 1.6 µm (± 0.36) (Fig. 57).

Picris hispanicus (1): Polar thickening: 10-16 spines. Paraporal lacunae: fugitives and polar spines occasionally invade. Equatorial ridge: unilinear, 5-7 spines per interporal segment. P/E ratio = 0.88, E.D. = 38.2 µm (± 1.9), P.D. = 33.7 µm (± 1.0), S.L. = 2.3 µm (± 0.29).

Urospermum (2/2)

Urospermum is a ditypic, stenopalynous genus. Shape: open interhexagonal, spherical to oblate. Polar thickening: variable in breadth and spininess, polar channels are common. Abporal lacunae:

large, oval to triangular. Paraporal lacunae: occasional fugitive spines. Equatorial ridge: unilinear, spine bases often partially free from adjacent spine bases. Polar-mesocopal ridge: well-defined.

Urospermum picroides (2): The 2 samples examined display considerable variation in some features. One is more spherical in equatorial view, bears more spines (9-18) on the polar thickening, and on each segment of the equatorial ridge. In the second sample the polar thickening bears 2-8 spines. P/E ratio = 0.88, E.D. = 38.9 μm (± 0.64), P.D. = 34.2 μm (± 1.8), S.L. = 2.0 μm (± 0.07).

Urospermum dalechampii (1): Polar thickening bears 3-9 spines. P/E ratio = 0.90, E.D. = 36.6 μm (± 2.7), P.D. = 33.1 μm (± 2.7), S.L. = 2.3 μm (± 0.34).

Endomorphology:

Exine stratification patterns in the Leontodontinae, as revealed by TEM, are relatively homogeneous and are typical of those found in most of the Lactuceae. Intergeneric variations are greater than the intrageneric differences but the total range of variation within the subtribe is small. In the paragraphs below, a subtribal description of typical exine stratification is given, followed by descriptions of each genus studied. When TEM data was obtained for more than one taxon per genus, any intrageneric differences are also noted. (See Figure 2 for a diagram of Leontodontinae endomorphological variations.)

Leontodontinae exines, like those of all Astereaceae, have a complex, electron dense outer wall, the ektexine, and the less electron dense inner wall, the endexine. A cavus, or small cavity, separates the foot layer (innermost ektexine) from the other elements of the ektexine. The

cavus is larger below the spines of the equatorial and paraporal ridges and narrow in the paraporal lacunae.

The ektexine (from outside to inside) consists of a spiny perforate tectum, one to many levels of solid columellae, and a foot layer. The spines are conical with blunt, nonperforate, apices with a single apical channel (Fig. 68), and globose, perforate bases. The spine bases and ridges contain ca 5-10 levels of anastomosing columellae. (The number of anastomosing layers must be approximated due to the intricate and often tangential branching of the rods.) The outermost layer of columellae are distinctly larger, non-anastomosing, evenly spaced and oriented radially with respect to the spine or ridge (Fig. 64). The innermost layer of columellae are partially fused to form a discontinuous infratectum under the spines. Lacunar columellae may consist of one level of distinct, erect rods (Fig. 67), or several levels of anastomosing rods (Fig. 66). These columellae may be completely fused at the base to form a continuous infratectum (Fig. 67), or only partially fused to form a discontinuous infratectum (Fig. 66). The infratectum of the spines and lacunae are periodically connected to the foot layer by means of small, oblique ektexinous rods. In some species, small erect columellae span the cavus to join the lacunar infratectum to the foot layer (Fig. 66). Under the spines, massive columellae span the cavus to attach to the foot layer (Fig. 60). These large rods may branch into the upper anastomosing layers, or extend up into the spine tips. They often line the central open area in the spine (Fig. 64). The foot layer is the innermost ektexine layer and caps the endexine. In most taxa fine foot layer lamellations are interbedded into the exdexine (Fig. 67). In some species, ektexinous lamellations are dispersed throughout the endexine (Figs. 68, 69). The endexine:foot layer ratio among the taxa ranges from 2:1 to 6:1.

The foot layer is thickest under the ridges and quite thin near the apertures. At the aperture only this thin foot layer covers a thickened endexine.

The endexine of most taxa appears to be of uniform density in the lacunar areas but is often highly disrupted into individual strands or reticulations under the ridges (Fig. 60). This disrupted condition is probably an artifact of the sectioning process. In one species of Hypochoeris the endexine is separated into indigeneous lamellae (Fig. 70), and in 3 other species of the same genus the endexine appeared to be of a distinctly heterogeneous or spongy texture (Figs. 68, 69). The endexine is thickest near the apertures and thinnest in the lacunae.

Aposeris: Spinal columellae: 8-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 3:1. Endexine is less disrupted in this genus (Fig. 67). (A. foetida)*

Garhadiolus: Spinal columellae: 9-11 levels. Lacunar columellae: 2 levels. Lacunar infratectum: discontinuous. Endexine:foot layer = 6:1. Endexine is less disrupted. (G. hedypnois)*

Hedypnois: Spinal columellae: 7-9 levels. Lacunar columellae: 1-2 levels. Lacunar infratectum: discontinuous. Endexine:foot layer = 4:1. Thick, erect rods connect the lacunar infratectum and foot layer. (H. cretica)*

Hyoseris: Spinal columellae: 7-8 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 5:1 (Fig. 65). (H. radiata ssp. radiata)*

*Designates the species from which the data were derived.

Hypochoeris

Hypochoeris tenuifolia (S. American/echinolophate): Spinal columellae: 8-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 5:1. Endexine is distinctly heterogeneous or spongy in texture.

Hypochoeris apargioides (S. American/mod. echinolophate): Spinal columellae: 9-11 levels. Lacunar columellae: 1 level. Lacunar infratectum: discontinuous. Endexine:foot layer = 2:1. The anastomosing columellae are much denser than in other taxa. Within spines, massive columellae are unusually frequent within the anastomosing layer, and also appear to surround the open area in the center of the spine base. These massive columellae are most developed in this taxon. The cavus under the spines and in the lacunae is minimal. The endexine under the spines contains indigenous lamellae (Fig. 70).

Hypochoeris arenaria v. andina (S. American/mod. echinolophate): Spinal columellae: 7-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: discontinuous. Endexine:foot layer = 4:1. The endexine contains ektexinous lamellations throughout, and appears to be uniquely heterogeneous or spongy in texture. The cavus is larger than in other taxa in both lacunae and under spines. Many small oblique rods connect the columellae to the foot layer (Figs. 68, 69).

Hypochoeris acaulis (S. American/subechinate): Spinal columellae: 7-8 levels. Lacunar columellae: 2 levels. Lacunar infratectum: continuous. Endexine:foot layer = 3:1. Like H. arenaria v. andina,

the cavus is greatly expanded and the oblique connecting rods are numerous (Fig. 61).

Hypochoeris elata (S. American/subechinate): Spinal columellae: 7-8 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 4:1. Endexine severely disrupted in some areas and heterogeneous in texture.

Hypochoeris laevigata (Medit. - N. Africa): Spinal columellae: 8-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 5:1. Endexine often appears spongy in texture.

Leontodon: Spinal columellae: 9-10 levels. Lacunar columellae: 1 level. Lacunar infratectum: usually continuous. Endexine:foot layer = 4:1. There is a lesser degree of microperforation in the lacunar tectum in this genus and the upper, more regular layer of columellae in the spines are taller. A more distinct order can be detected in the orientation of the anastomosing layers than is typical of other taxa. The short thick columellae that periodically join the lacunar infratectum to the foot layer are numerous and erect (Figs. 63, 64). (L. hirsutus, L. incanus, L. laciniatus, L. maroccanus)*

Picris:

Picris hieracioides: Spinal columellae: 8-10 levels. Lacunar columellae: 1 level. Lacunar infratectum: discontinuous. Endexine:foot layer = 4:1 (Figs. 58, 59, 66). (ssp. hieracioides and squarrosus)*

Picris echioides: Spinal columellae: 9-10 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous, thin. Endexine:foot layer = 3:1.

Picris strigosa: Spinal columellae: 8-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: discontinuous. Endexine:foot layer = 3:1.

Picris damascena: Spinal columellae: 8-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: discontinuous. Endexine:foot layer = 5:1.

Picris hispanicus: Spinal columellae: 9-10 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 3:1.

Rhagadiolus: Spinal columellae: 8-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 3:1. (R. stellatus)*

Urospermum: Spinal columellae: 8-9 levels. Lacunar columellae: 1 level. Lacunar infratectum: continuous. Endexine:foot layer = 5:1. The foot layer surface adjacent to the endexine is often rough (Fig. 60). (U. picroides, U. dalechampii)*

Figure 58. SEM micrograph of the aperture region of Picris hieracioides ssp. hieracioides, Tiiden 803 (F). Line equals 1 µm.

Figure 59. TEM micrograph of P. hieracioides ssp. hieracioides exine, section through the paraporal ridge (tangential), Polunin 6425 (F). Note the increase in columellae size nearer to the aperture. Line equals 1 µm.

Figure 60. TEM micrograph of Urospermum picroides exine, cross section through part of the equator near an aperture, Lazar 504 (F). Arrow indicates aperture. Line equals 1 µm.

Figure 61. TEM micrograph of Hypochoeris acaulis exine, section through the equator, Eyerdam 25059 (F). Arrows indicate the 3 apertures. Line equals 5 µm.

Figure 62. SEM micrograph of a broken grain of Hypochoeris taraxacoides, revealing the columellar structures within a spine, Buchtien s.n. (NY). Line equals 1 µm.

Figure 63. TEM micrograph of Leontodon laciniatus exine, a nearly equatorial section, Barkley & Palmatier 1068 (F). Line equals 5 µm.

Figure 64. TEM micrograph of L. maroccanus exine, cross section through a spine, P. & J. Davis 48207 (NY). Arrow indicates the central open space and the massive columellae lining it. Line equals 1 µm.

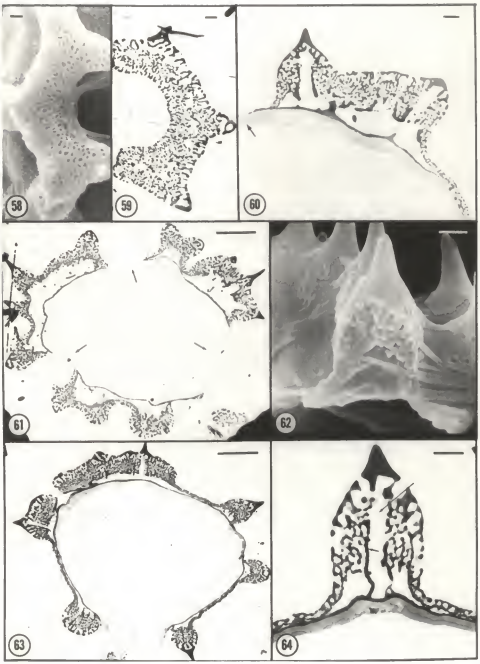
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Figure 65. TEM micrograph of Hyoseris radiata ssp. radiata exine, cross section through the aperture region, Bourgeau s.n. (F). Line equals 5 µm.

Figure 66. TEM micrograph of Picris hieracioides ssp. hieracioides exine, cross section through the tectum of the paraporal lacuna, Chessman s.n. (NY). Arrows indicate the erect vertical rod connecting the foot layer and infratectum, the discontinuous infratectum and anastomosing lacunar columellae. Line equals 1 µm.

Figure 67. TEM micrograph of Aposeris foetida exine, cross section, Tscherning s.n. (F). Arrows indicate the continuous infratectum and foot layer lamellations in the endexine. Line equals 1 µm.

Figure 68. TEM micrograph of Hypochoeris arenaria v. andina exine showing large cavus, ektexinous lamellations throughout the heterogeneous endexine. Stork & Horton 10245 (F). Line equals 1 µm.

Figure 69. TEM micrograph of H. arenaria v. andina exine, section through a ridge showing oblique rods within the cavus and ektexinous lamellations throughout the endexine. Line equals 1 µm.

Figure 70. TEM micrograph of Hypochoeris apargioides exine, section through a ridge showing the massive columellae and indigeneous lamellae of the endexine, Vargas 11013 (F). Line equals 1 µm.

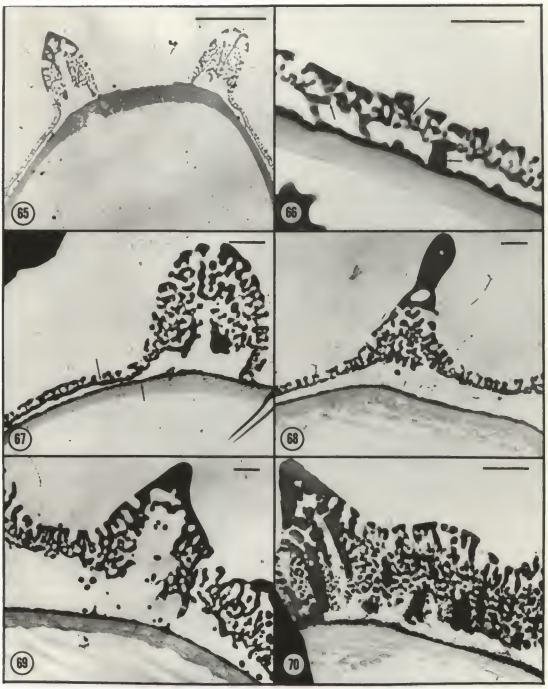
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Table 2

Pollen Grain Measurements

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
Aposeris foetida Neck (NY)	40.8 ± 1.7 (38.1 - 44.5)	37.1 ± 1.3 (34.3 - 39.4)	2.8 ± 0.31 (2.3 - 3.4)	0.91
Tscherning (F)	39.5 ± 2.3 (34.5 - 43.9)	38.1 ± 2.0 (34.5 - 42.3)	2.9 ± 0.31 (2.4 - 3.1)	0.96
Andrews (NY)	38.3 ± 1.5 (34.3 - 40.6)	35.5 ± 1.5 (31.8 - 38.1)	2.6 ± 0.42 (1.9 - 3.5)	0.93
Italy (NY)	37.9 ± 1.4 (34.3 - 40.6)	36.1 ± 1.0 (34.3 - 38.1)	2.6 ± 0.34 (1.9 - 3.2)	0.95
Garhadiolus hedypnois Myers (F)	37.4 ± 2.7 (34.3 - 41.9)	34.3 ± 2.3 (30.5 - 39.4)	2.2 ± 0.46 (1.3 - 3.2)	0.92
	* 45.1 ± 1.7 (43.2 - 48.3)	39.5 ± 1.4 (38.1 - 41.9)	2.7 ± 0.27 (2.5 - 3.2)	0.88
G. papposus Africa (NY)	30.9 ± 1.7 (27.9 - 34.3)	27.9 ± 1.4 (25.4 - 30.5)	1.6 ± 0.32 (1.3 - 1.9)	0.90
Hedypnois cretica Reverchon (NY)	34.5 ± 2.0 (30.5 - 38.1)	32.1 ± 1.9 (27.9 - 35.6)	2.0 ± 0.26 (1.9 - 2.5)	0.93
	* 42.4 ± 2.1 (38.1 - 47.0)	36.6 ± 1.2 (34.3 - 38.1)	2.2 ± 0.32 (1.9 - 2.5)	0.86

*Tetracolporate measurements

Table 2 (continued)

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
R. B. Streets (NY)	35.7 ± 1.3 (33.0 – 38.1)	31.8 ± 1.3 (29.2 – 34.3)	2.2 ± 0.30 (1.9 – 2.5)	0.89
	* 41.3 ± 1.6 (39.4 – 43.2)	35.6 ± 0.80 (34.3 – 36.8)	2.2 ± 0.30 (1.9 – 2.5)	0.86
Willis (F)	34.5 ± 2.8 (29.2 – 40.6)	30.2 ± 2.2 (26.7 – 35.6)	2.2 ± 0.46 (1.3 – 3.2)	0.88
	* 41.4 ± 2.2 (36.8 – 44.5)	37.7 ± 2.5 (34.3 – 41.9)	2.2 ± 0.30 (1.9 – 2.5)	0.91
Benke (F)	34.4 ± 2.4 (31.8 – 39.4)	30.3 ± 1.9 (26.7 – 33.0)	2.0 ± 0.38 (1.3 – 2.5)	0.88
	* 43.9 ± 2.7 (40.6 – 49.5)	38.7 ± 1.4 (36.8 – 40.6)	2.0 ± 0.50 (1.3 – 3.2)	0.88
H. monspeliensis Font Quer (NY)	37.5 ± 1.7 (34.3 – 41.9)	33.5 ± 1.1 (31.8 – 35.6)	2.5 ± 0.91 (1.9 – 2.5)	0.89
H. pendula Chanpenfier (NY)	40.3 ± 1.5 (36.8 – 43.2)	37.5 ± 1.8 (33.0 – 40.6)	2.3 ± 0.43 (1.3 – 3.2)	0.93
H. radiata ssp. graeca P. & J. Davis (NY)	39.8 ± 2.3 (35.6 – 42.5)	36.2 ± 1.6 (31.8 – 38.1)	2.4 ± 0.20 (2.2 – 2.7)	0.91
H. radiata ssp. radiata Bourgeau (F)	39.5 ± 2.8 (34.3 – 44.5)	36.3 ± 2.1 (33.0 – 40.6)	2.3 ± 0.29 (1.9 – 2.7)	0.92

Table 2 (continued)

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
Canut (NY)	39.1 ± 1.4 (36.8 - 41.9)	36.4 ± 1.3 (34.3 - 40.0)	2.3 ± 0.27 (1.9 - 2.5)	0.93
Choulette (NY)	37.9 ± 1.7 (34.3 - 40.6)	35.4 ± 1.4 (33.0 - 38.1)	2.1 ± 0.31 (1.3 - 2.5)	0.93
Hypochoeris acaulis Eyerdam (F)	41.6 ± 2.4 (36.8 - 44.5)	37.0 ± 1.6 (34.3 - 40.6)	3.1 ± 0.48 (2.5 - 3.8)	0.89
	* 46.9 ± 4.8 (38.1 - 53.3)	40.2 ± 3.4 (34.3 - 44.5)	3.0 ± 0.62 (2.5 - 3.8)	0.86
H. achyrophorus Pitard (NY)	31.0 ± 1.7 (26.7 - 33.0)	28.3 ± 1.6 (25.4 - 31.8)	1.9 ± 0.35 (1.3 - 2.5)	0.91
H. aparagioides Vargas (F)	35.8 ± 1.7 (31.4 - 39.2)	30.7 ± 1.4 (25.9 - 33.7)	2.7 ± 0.48 (1.9 - 3.9)	0.86
H. arenaria ssp. andina Stork & Horton (F)	41.9 ± 2.9 (36.2 - 47.6)	36.9 ± 2.0 (32.9 - 41.3)	3.7 ± 0.39 (3.1 - 4.5)	0.88
H. cretensis Rechinger (US)	35.0 ± 1.4 (31.8 - 38.1)	31.8 ± 0.71 (29.8 - 33.0)	2.1 ± 0.30 (1.7 - 2.9)	0.91
H. elatà McBride & Featherstone (F)	36.3 ± 1.4 (33.3 - 40.0)	31.9 ± 1.4 (29.0 - 35.3)	2.5 ± 0.26 (2.0 - 3.1)	0.88
H. glabra Radford (NY)	29.0 ± 1.6 (25.4 - 31.8)	26.9 ± 0.95 (25.4 - 29.2)	1.5 ± 0.16 (0.98 - 1.7)	0.93
Samuelsson (NY)	30.0 ± 1.5 (26.7 - 33.0)	27.9 ± 1.3 (25.4 - 30.5)	1.8 ± 0.27 (1.2 - 2.4)	0.92

Table 2 (continued)

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
H. grandiflora Hsia (NY)	58.2 ± 3.8 (52.0 - 68.6)	53.3 ± 3.0 (48.3 - 59.7)	4.0 ± 0.49 (3.2 - 5.1)	0.92
H. hohenackeri Cazalet & Pennington (NY)	43.1 ± 1.8 (39.4 - 45.7)	40.8 ± 1.5 (38.1 - 43.2)	3.8 ± 0.60 (2.5 - 5.1)	0.95
H. laevigata P. & J. Davis (NY)	30.7 ± 1.4 (27.9 - 34.3)	27.9 ± 1.3 (25.4 - 31.8)	1.6 ± 0.32 (1.3 - 1.9)	0.91
H. lutea Hatschbach (NY)	36.6 ± 2.0 (31.8 - 39.4)	34.5 ± 1.9 (30.5 - 38.1)	2.9 ± 0.52 (1.9 - 3.8)	0.94
H. microcephala v. microcephala Wolston (GH)	38.2 ± 2.1 (34.3 - 43.2)	34.8 ± 1.8 (31.8 - 39.4)	2.6 ± 0.39 (1.9 - 3.8)	0.97
H. microcephala v. albiflora Shinners (GH)	36.2 ± 2.5 (31.8 - 44.5)	33.2 ± 2.1 (30.5 - 38.1)	2.9 ± 0.43 (2.5 - 3.8)	0.92
H. radicata Nelson & Kimball (NY)	31.6 ± 2.5 (26.7 - 35.6)	30.1 ± 1.1 (27.9 - 31.8)	1.8 ± 0.32 (1.3 - 2.5)	0.95
H. taraxacoides Buchtien (NY)	45.0 ± 2.1 (40.6 - 49.5)	43.4 ± 2.2 (38.1 - 48.3)	4.3 ± 0.71 (2.5 - 6.4)	0.96
H. tenuifolia Pandel (NY)	42.3 ± 2.1 (38.1 - 48.3)	37.7 ± 1.2 (35.6 - 39.4)	2.9 ± 0.43 (2.5 - 3.8)	0.89
H. tweediei Ward (NY)	34.4 ± 1.7 (31.8 - 36.8)	30.9 ± 1.8 (27.9 - 34.3)	2.5 ± 0.41 (1.7 - 3.4)	0.90
	* 35.6 ± 2.1 (32.4 - 39.4)	32.9 ± 2.3 (29.2 - 36.8)	2.2 ± 0.33 (1.9 - 2.5)	0.92

Table 2 (continued)

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
H. uniflora Werdermann & D. Meyer (US)	46.9 ± 2.0 (43.2 – 50.8)	42.8 ± 2.1 (39.4 – 47.0)	3.0 ± 0.45 (2.5 – 3.8)	0.91
H. variegata Fabris (NY)	38.3 ± 2.2 (31.8 – 44.5)	36.4 ± 1.7 (33.0 – 39.4)	2.8 ± 0.35 (1.9 – 3.2)	0.95
Leontodon autumnalis Gillett & Findlay (US)	36.1 ± 1.4 (33.0 – 38.1)	38.6 ± 2.3 (34.9 – 43.8)	2.8 ± 0.47 (2.2 – 3.9)	0.93
L. crispus ssp. asperrimus Samuelsson (NY)	39.8 ± 1.6 (36.8 – 43.2)	35.1 ± 1.4 (31.8 – 38.1)	2.5 ± 0.36 (1.9 – 3.2)	0.88
L. crispus ssp. crispus Thomas (NY)	37.2 ± 1.5 (34.3 – 39.4)	34.4 ± 1.2 (31.8 – 36.8)	2.1 ± 0.35 (1.3 – 2.5)	0.92
L. crispus ssp. crispus (L. asper) Bornmuller (NY)	36.8 ± 1.5 (34.3 – 39.4)	34.1 ± 1.6 (31.8 – 38.1)	2.3 ± 0.34 (1.9 – 3.2)	0.93
L. hirsutus Kaspicw (F)	39.2 ± 1.7 (34.9 – 41.9)	33.6 ± 1.6 (27.9 – 36.8)	2.4 ± 0.41 (1.3 – 3.2)	0.86
L. hispidus E. Moldenke (NY)	41.1 ± 2.4 (36.8 – 45.7)	37.2 ± 1.9 (34.3 – 40.6)	2.3 ± 0.34 (1.9 – 3.2)	0.90
L. incanus Jeaupert (F)	41.3 ± 3.3 (32.4 – 45.7)	35.7 ± 2.2 (31.8 – 39.4)	2.7 ± 0.36 (1.9 – 3.8)	0.86
L. laciniatus Barkley & Palmatier (F)	33.2 ± 2.6 (27.9 – 38.1)	30.5 ± 2.5 (25.4 – 34.3)	2.0 ± 0.37 (1.3 – 2.5)	0.92
Lazar (F)	34.9 ± 2.5 (27.9 – 39.4)	31.0 ± 2.2 (26.7 – 34.3)	2.1 ± 0.35 (1.3 – 2.5)	0.89

Table 2 (continued)

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
L. maroccanus P. & J. Davis (NY)	36.7 ± 1.2 (33.0 – 38.1)	33.0 ± 1.1 (30.5 – 35.6)	1.8 ± 0.26 (1.3 – 1.9)	0.90
L. saxatilis ssp. saxatilis Dansereau, Pinto, Da Silva & Rainha (NY)	36.4 ± 1.1 (34.3 – 38.1)	32.2 ± 0.90 (30.5 – 34.3)	2.0 ± 0.41 (1.3 – 3.2)	0.88
Picris echioides Eichler (NY)	36.9 ± 2.1 (31.8 – 39.4)	33.9 ± 1.5 (30.5 – 36.8)	2.3 ± 0.36 (1.9 – 3.2)	0.92
De Toni (NY)	40.1 ± 1.1 (38.1 – 41.9)	37.7 ± 1.5 (35.6 – 40.6)	2.1 ± 0.34 (1.3 – 2.5)	0.94
P. damascena v. homocarpa Samuelsson (NY)	36.7 ± 1.6 (33.0 – 39.4)	32.9 ± 1.1 (30.5 – 35.6)	1.6 ± 0.36 (1.3 – 2.5)	0.90
P. hieracioides ssp. hicracioides O. Polunin (F)	41.0 ± 2.0 (34.3 – 44.5)	36.0 ± 1.4 (33.0 – 38.1)	2.8 ± 0.39 (1.9 – 3.8)	0.88
Tilden (F)	41.1 ± 1.6 (38.1 – 44.5)	35.9 ± 1.5 (33.0 – 39.4)	2.5 ± 0.44 (1.3 – 3.2)	0.87
New South Wales (NY)	41.5 ± 2.4 (38.1 – 46.4)	38.1 ± 1.3 (35.6 – 40.6)	2.7 ± 0.27 (1.2 – 3.2)	0.92
Chessman (NY)	38.4 ± 1.6 (34.3 – 40.6)	35.0 ± 1.1 (33.0 – 36.8)	2.3 ± 0.30 (1.9 – 2.5)	0.91

Table 2 (continued)

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
Pallon (NY)	44.7 ± 2.4 (39.4 – 49.5)	39.0 ± 1.5 (35.6 – 41.9)	2.8 ± 0.39 (1.9 – 3.5)	0.87
P. hieracioides ssp. japonica Murata (NY)	37.0 ± 1.7 (34.3 – 41.9)	33.1 ± 1.4 (30.5 – 35.6)	2.5 ± 0.31 (1.9 – 3.2)	0.89
P. hieracioides ssp. kamtschatica Robert Hardy (NY)	38.2 ± 1.8 (35.6 – 41.9)	35.0 ± 1.7 (31.8 – 39.4)	2.8 ± 0.42 (1.9 – 3.8)	0.92
P. hieracioides ssp. squarrosus Kaspiew (F)	42.4 ± 1.3 (38.1 – 44.5)	37.0 ± 1.6 (34.3 – 39.4)	2.6 ± 0.29 (1.9 – 3.2)	0.88
P. hieracioides ssp. villarsii Sweden (NY)	38.3 ± 1.1 (35.6 – 39.4)	34.4 ± 0.77 (33.0 – 35.6)	2.5 ± 0.35 (1.9 – 3.2)	0.90
P. hispanicus P. & J. Davis (NY)	38.2 ± 1.8 (33.0 – 40.6)	33.7 ± 1.0 (30.5 – 35.6)	2.2 ± 0.29 (1.9 – 2.5)	0.88
P. strigosa Meyer & Dinsmore (F)	39.4 ± 1.1 (38.1 – 41.9)	34.1 ± 1.1 (31.2 – 35.6)	2.3 ± 0.40 (1.6 – 3.2)	0.86
Rhagadiolus stellatus Amdursky (GH)	34.0 ± 1.6 (31.8 – 36.8)	31.5 ± 1.4 (29.3 – 34.3)	2.1 ± 0.26 (1.9 – 2.5)	0.92
Meyers & Dinsmore (F)	33.0 ± 1.2 (30.5 – 35.6)	30.1 ± 1.0 (27.3 – 31.8)	2.3 ± 0.29 (1.9 – 2.5)	0.91
Urospermum dalechampii Reverchon (NY)	36.6 ± 2.7 (31.8 – 41.9)	33.1 ± 2.6 (27.9 – 38.1)	2.3 ± 0.34 (1.9 – 3.2)	0.90
U. picroides Lazar (F)	39.3 ± 1.6 (35.6 – 41.3)	35.5 ± 1.9 (33.0 – 39.4)	1.9 ± 0.46 (1.3 – 2.5)	0.90

Table 2 (continued)

Taxon	Mean Equatorial Diameter µm	Mean Polar Diameter µm	Mean Spine Length µm	Polar Diameter/ Equatorial Diameter
Jeaupert (F)	38.4 ± 1.7 (35.6 – 41.9)	32.9 ± 1.4 (30.5 – 35.6)	2.0 ± 0.36 (1.3 – 2.5)	0.86

DISCUSSION

The taxonomic boundaries of the Leontodontinae have long been a subject of dispute. There is little disagreement concerning the alliance of Picris, Leontodon, Hypochoeris and Urospermum, but the taxonomic affinities of Hyoseris, Aposeris, Hedypnois, Rhagadiolus, and Garhadiolus are obscure and somewhat controversial. Stebbins (1953) erected the subtribe Leontodontinae to include those genera with coarse, spreading, hirsute pubescence, often of forked hairs, paleaceous or naked receptacle, yellow flowers, fusiform or beaked achenes, coarse, plumose pappus (occasionally paleaceous or coroniform), elongate style branches and echinolophate pollen. He assigned Aposeris and Hyoseris to the Crepidinae and Cichorinae, respectively. Stebbins regarded Aposeris as a specialized, epappose offshoot of the Youngia-Ixeris complex within the Crepidinae, and Hyoseris as an isolated genus in the Cichorinae, showing no clear relationship to other genera in the subtribe. In a slightly different treatment of this group, Jeffrey (1966) erected the Hypochoeris Subgroup and divided it into 2 series. In the Hypochoeris-Series he acknowledged affinities among Picris, Hypochoeris, Leontodon, Urospermum, Garhadiolus, Rhagadiolus and Hedypnois on the basis of their hispid pubescence, rough achenes, and basic chromosome number of seven. Jeffrey assigned Aposeris and Hyoseris to the Hyoseris-Series, characterized by glabrous herbage, smooth achenes with hairy margins, and a basic chromosome number of eight.

The pollen exomorphology and endomorphology of the Leontodontinae (sensu Stebbins) firmly support its stance as a cohesive taxonomic assemblage. The relatively little diversity encountered in internal and external wall characters reaffirms the boundary lines drawn by Stebbins and Jeffrey when they erected the Leontodontinae and Hypochoeris-Series, respectively.

These pollen data also lend credence to Jeffrey's disposition of Aposeris and Hyoseris into the Hypochoeris Subgroup. The very traits that distinguish the pollen of these two genera from most of the Leontodontinae, i.e., extreme reduction of the polar thickening and the occurrence of polar lacunae, are in fact common to several species of the subtribe. Thus, at the very least, pollen characters cannot be employed to exclude Aposeris and Hyoseris from the Leontodontinae.

The extremes of diversity in both endo- and exomorphology are found in Hypochoeris, the largest and most primitive genus in the Leontodontinae. The 50 (Stebbins et al., 1953) to 100 (Cabrera, 1963) species also exhibit considerable morphological and karyotypic diversity, and have been the subject of much study.

Hypochoeris was subdivided by Hoffman (1891) into 5 well-marked sections, based on modifications of the achenes and pappus. The unusual geographic distribution of the members of each of Hoffman's sections, and karyotypic analyses aided Stebbins (1971) in postulating a center of diversity of the genus. Stebbins determined that seven species are indigenous to the Mediterranean, North Africa and Western Asia, two to the Alps, Caucasus and mountains of central Asia, one to Eastern Asia, and more than 40 to South America. Those species that are indigenous to Asia and South America are all members of the most primitive section, Achyrophorous, while all the other sections are represented only in the Mediterranean region and the Alps. Karyotypic analyses of species from each area enabled Stebbins to identify western Eurasia as the center of diversity of Hypochoeris and related genera, Picris and Leontodon. Stebbins found that the South American species of Hypochoeris have specialized karyotypes of n=4 and that continent probably possesses a secondary center of diversity of the genus.

Pollen morphology is of minimal use in confirming section boundaries within Hypochoeris. The widely distributed echinolophate species are variable in pollen size, and sculpturing features and size of the polar thickening, but the 5 sections are not clearly distinguished by possession of definite ranges of pollen variability. Moreover, the modified echinolophate and subechinate species are all members of the Achyrophorous section, a section which includes echinolophate species as well. Table 3 summarizes the geographic distribution, sculpturing pattern, chromosome number (if known), and section identities of each taxon.

Only species of section Achyrophorous were found to be distinct from the other sections in terms of pollen morphology. The subechinate and modified echinolophate South American species are easily distinguishable from the invariably echinolophate pollen of other sections. But the echinolophate Achyrophorous differed from other sections only in their distinctly larger mean equatorial diameters and spine lengths (Table 3).

The large size, long spines and echinate sculpture of Lactuceae pollen is thought to be a reflection of a primitive nature (Tomb, 1975). The fact that evidences of these 3 traits have been identified in Achyrophorous seems to substantiate the section's relative primitiveness. The diversity in pollen morphology in the section in South America reflects the great amount of adaptive radiation that has occurred on that continent. In light of Stebbins' conclusion that South America possesses a secondary center of diversity of the genus, it may well be that the modified echinolophate and subechinate sculpturing patterns of the South American species may be secondarily derived from the echinolophate mode.

The remaining 3 sections of Hypochoeris cannot readily be segregated from each other using only features of pollen exomorphology. The pollen of H. cretensis of section Metabasis is in fact intermediate in size and

Table 3

Hypochoeris

Taxon	Distribution	Section	Sculpture	E.D. (µm)	S.L. (µm)	n=
H. achyrophorous	Mediterranean	Seriola	El[a]	31	1.9	6
H. laevigata	Italy, Sicily N. Africa	--	El	31	1.1	-
H. cretensis	Mediterranean-Alps	Metabasis	El	35	2.2	3
H. glabra	Cosmopolitan	EuHypochoeris	El	30	1.6	5
H. radicata	Cosmopolitan	EuHypochoeris	El	32	1.8	4
H. grandiflora	E. Asia	Achyrophorous	El	58	4.0	5
H. uniflora	C. Europe - Ukraine	Achyrophorous	El	47	3.1	5
H. tenuifolia	S. America	Achyrophorous	El	42	2.9	-
H. variegata	S. America	Achyrophorous	El	38	2.8	-
H. lutea	S. America	Achyrophorous	El	37	2.9	-
H. apargioides	S. America	Achyrophorous	mEl[b]	36	2.7	-
H. arenaria v. andina	S. America	Achyrophorous	mEl	42	3.7	-
H. hohenackeri	S. America	Achyrophorous	mEl[c]	43	3.8	-
H. microcephala	S. America	Achyrophorous	sEc	38	2.6	-
H. microcephala v. albiflora	S. America	Achyrophorous	sEc	36	2.9	-
H. acaulis	S. America	Achyrophorous	sEc	42	3.0	-
H. tweediei	S. America	Achyrophorous	sEc	34	2.2	4
H. elata	S. America	Achyrophorous	sEc	36	2.5	4
H. taraxacoides	S. America	Achyrophorous	sEc	45	4.3	-

[a] Echinolophate

[b] Modified echinolophate

[c] Subechinate

spine length between that of section Achyrophorous and those of Seriola and EuHypochoeris. But the pollen of all sections except Achyrophorous have unilinear ridges, large, vacant lacunae and differ only vaguely from each other in the fine details of polar sculpturing. Thus, in terms of pollen exomorphology, these 3 sections form a homogeneous assemblage.

The endomorphology of Hypochoeris pollen, like its exomorphology, is more heteromorphic than other genera of the subtribe. Endomorphological data are not as complete as exomorphological, but the results show several species of South American Hypochoeris to diverge from the highly consistent Leontodontinae exine stratification. Hypochoeris apargioides is distinguished by its high endexine:foot layer ratio, thickened columellae and lamellate endexine. Hypochoeris arenaria v. andina and H. acaulis are distinguished by an unusually extensive cavus and numerous oblique connecting rods between the tectum and foot layer, and ektexinous lamellations throughout the endexine. Hypochoeris elata, H. arenaria v. andina, H. acaulis, H. laevigata and H. tenuifolia all possess a distinctive endexine of a heterogeneous texture (Figs. 68, 69).

In summary, the pollen exomorphology of Hypochoeris substantiates the primitiveness of the Achyrophorous section of the genus, i.e., by their large size, long spines, and the increased spininess of some species. The diversity of pollen forms in South America, i.e., echinolophate, modified echinolophate and subechinate, probably reflects the great amount of adaptive radiation that has occurred in Hypochoeris on that continent. It is uncertain as to whether the modified echinolophate and subechinate forms, supposedly more primitive, may in fact be secondarily derived from the echinolophate forms. The subechinate and modified echinolophate pollen studied was also distinctive from echinolophate forms in

endomorphology but this, too, is inconclusive in regard to their relative primitiveness.

Leontodon is a large genus of ca 40 species native to Europe, Western Asia, North Africa and the Azores. It is a close relative of Picris and Hypochoeris, separated from the latter by the receptacular scales of Hypochoeris, and from the former by leaf arrangement and type of indumentum. Leontodon lacks hooks on the arms of branched hairs that are typical to Picris and it is usually scapose (Sell, 1975). But geographic variability in these distinguishing characters sometimes increases the difficulty of segregating Picris and Leontodon. In fact, Sell maintains that the Leontodon subgenus of Leontodon (few cauline bracts, branched hairs) may actually be more closely related to Picris than to the Apargia subgenus of Leontodon (numerous cauline bracts, simple hairs). Recent work by Widder (1931, 1967) and Rousi (1973) has helped to clarify the cytotaxonomy and nomenclatural confusion of Leontodon but extensive biosystematic revision is needed.

Various authors have proposed taxonomic subdivisions of Leontodon (Hegi, 1928; Widder, 1931; Ball, 1850; Hoffman, 1891; Holub & Moravec, 1952) but those of Widder, culminating 4 decades of study, seems most natural in light of subsequent chromosomal studies. Widder's classification scheme (see Table 4) is employed here.

Rousi (1973) described Widder's section Asterothrix as the most primitive section of the genus and karyotypic data seem to support this. Stebbins (1953) pointed out that the evolution of karyotype modification in the Lactuceae includes trends toward decrease in the basic number of chromosomes, smaller chromosomes and an increase in assymetry of the karyotype. Rousi (1973) found several of these primitive features to be characteristic of the species of the section Asterothrix, e.g., relatively high numbers of large chromosomes and often symmetrical karyotypes.

Table 4

LEONTODON (Widder's Classification Scheme)
Chromosomal and Pollen Variability

	x=	E.D. (µm)	S.L. (µm)
Subgenus Leontodon			
Section Leontodon			
L. autumnalis	6	36	2.8
Section Rostrati			
L. laciniatus	6	34	2.1
Subgenus Apargia			
Section Asterothrix			
L. crispus s. crispus	4	37	2.1
L. asper	4	37	2.4
L. crispus s. asperrimus	4	40	2.5
L. hispidus	7	41	2.4
L. incanus	4	41	2.7
Section Thrincia			
L. saxatilis	4	36	2.0
L. maroccanus	-	37	1.8

Pollen morphology also appears to substantiate the primitive nature of the section Asterothrix. Tomb (1975) suggested that 3 evolutionary trends are apparent in the Lactuceae pollen grains forms: (1) development of echinolophate from echinate pollen, (2) decrease in pollen size, and (3) reduction in spine length and internal complexity in advanced taxa. The pollen of the member species of Asterothrix is relatively larger and spinier, i.e., abundant fugitive and polar spines encorach into the paraporal lacunae. This tendency toward occlusion of lacunae by spines may well reflect a proximity to the supposedly primitive echinate mode of sculpturing. Rousi considers L. hispidus to be still more primitive because of its high chromosome number (x=7), large and often metacentric chromosome, and horizontal rhizome, but the pollen of L. hispidus is essentially identical to that of other section members.

The pollen of Widder's sections Leontodon, Rostrati, and Thrincia (Hirsutus Group of this study) is relatively smaller and less spiny compared to Asterothrix, and possesses large, vacant lacunae, polar channels and/or polar lacunae within the small, sparsely spined polar thickening. Their pollen may be described as further removed from the echinate sculpturing pattern and, thus, presumably more phylogenetically advanced, as Rousi also concluded. Rousi viewed Thrincia as the most highly advanced section, followed in order by Rostrati, Leontodon, and finally Asterothrix. But because pollen exo- and endomorphology of the representatives of Thrincia, Rostrati, and Leontodon is nearly identical, these data reveal little about their evolutionary position.

If relative spininess and reduced size of pollen grains may be taken as an index of primitiveness, then the pollen data of Leontodon can lend credence to Rousi's phylogenetic interpretation (using karyotypic analyses) for Widder's classification scheme. But pollen morphology does

not identify Widder's section boundaries in Leontodon. Of the species examined here, only those pollen grains of species in section Asterothrix were fairly distinct from other sections, due to their generally larger size and slightly occluded lacunae, but all were endomorphologically alike.

The genus Picris is comprised of 40-50 species that are indigenous to the Old World although now naturalized in many regions of the world. Picris is closely allied to Leontodon and the two are commonly distinguished on the basis of what have proved to be geographically unstable characters. P. D. Sell (1975), as mentioned earlier, used the presence of cauline leaves and hooks on the branches of forked hairs to identify the European Picris. He recognized that cauline leaves do occur in Anatolian Leontodons, but nevertheless, transferred Leontodon hispanicus to Picris based on its possession of these 2 features. The pollen of the two genera are essentially identical although in this study Picris grains are shown to be slightly larger. Their respective ranges of intrageneric variation are also similar. Therefore, palynological evidence does not substantiate Sell's hypothesis that species of subgenus Leontodon may actually be closer to Picris than to the Leontodon subgenus Apargia.

The data summarized in Table 5 illustrates the minimal utility of pollen characters in identifying the section boundaries set forth by Hoffman (1891). He used the characters of the achenes and involucral bracts to subdivide Picris into four sections, three of which are represented in this investigation. There is considerable overlap in the variable features of pollen morphology among the species of sections EuPicris, Helminthia, and Spitzellia. The pollen of P. damascena (Spitzellia) is somewhat distinct because of its small size and shorter spines but this divergence from the morphology of the other sections is slight and perhaps inconsequential.

Table 5

Picris Pollen Data

Taxon	Locality	Section	No. Polar Spines	Fugitive Spines	E.D. (μm)	S.L. (μm)	Paraporal Lacunae
P. hieracioides							
s. *hieracioides*	Pakistan	EuPicris	7-14	occasional	41	2.8	small
s. *hieracioides*	New S. Wales	EuPicris	5-12	common	41	2.7	small
s. *hieracioides*	Australia	EuPicris	6-12	common	41	2.5	medium
s. *hieracioides*	New Zealand	EuPicris	12-17	rare	38	2.3	medium
s. *hieracioides*	Russia	EuPicris	4- 9	absent	45	2.8	large
s. *squarrosus*	Australia	EuPicris	7-12	common	42	2.6	medium
s. *japonica*	Japan	EuPicris	4-10	rare	37	2.5	medium
s. *kamtschatica*	Alaska	EuPicris	3- 8	occasional	38	2.8	small
s. *villarsii*	Sweden	EuPicris	4- 8	absent	38	2.5	large
P. hispanicus	Morocco	EuPicris	10-16	occasional	38	2.3	medium
P. strigosa	Palestine	EuPicris	7- 9	absent	39	2.3	large
P. echioides	Australia/ Italy	Helminthia	2-10	absent	39	2.2	large
P. damascena	Syria	Spitzellia	3-12	absent	37	1.6	large

In this investigation, Picris hieracioides serves as a vehicle to examine the relative degree of pollen variation that occurs at and below the species level. Analysis of 5 subspecies revealed that minor ('minor' because all species are echinolophate) variations in sculpturing among the subspecies are extensive. Moreover, the variability found in 5 samples of spp. hieracioides is equally as great. And furthermore, the degree of interspecific variation within the genus is comparable to intraspecific diversity. The extent of geographic variation in pollen morphology is similar. These data are summarized in Table 5 and Figs. 49-57.

In summary, this study of pollen variation at several taxonomic levels, i.e., interspecific, intraspecific, infraspecific, and in relation to geographic distribution, revealed pollen characters to be equally as heteromorphic as macromorphological features. Although trends in sculpturing features are often readily identifiable, minor variations in pollen occur not only among species of a genus, but among subspecies, within a single subspecies, and even among individual grains from the same capitulum.

Urospermum is a ditypic genus that is indigenous to the Mediterranean region, southwest Europe and Asia Minor. It is allied to Hypochoeris, Leontodon, and Picris because of the plumose, often basally swollen pappus hairs found in all 4 genera, but is easily distinguished from the 3 large genera by its complex, beaked achenes and single row of basally connate involucral bracts (Sell, 1975).

The pollen grains of the 2 species of Urospermum are essentially indistinguishable from those of Leontodon, Picris, and Old World Hypochoeris, that possess high, unilinear ridges, and large, generally vacant lacunae. The size and sculpturing of the polar region is equally heteromorphic in all 4 genera. These pollen data thus support previous authors' conclusions concerning the interrelatedness of the genera.

The taxonomic affinities of Aposeris, Hyoseris, and Rhagadiolus can be somewhat refined by consideration of the pollen morphology of the genera. The overall exo- and endomorphology is typical of the Leontodontinae. The epappose taxa, Aposeris and Rhagadiolus, are further distinguished by the absence of a polar thickening. In their case, the polar region exists only as a tripartite spined ridge formed by the confluence of the ridges which converge at the pole. This feature of radical reduction of the polar thickening is unique to Aposeris and Rhagadiolus among the taxa investigated in this study. This similarity may reflect a relationship between the genera or may instead be a case of parallel advancement. Hyoseris also exhibits a type of reduction in the polar thickening. In H. radiata ssp. radiata 3 small lacunae are incorporated into the polar thickening at the corners and separated by a few centrally located spines. This feature is not as well developed in ssp. graeca but it is still indicative of the trend toward reduction of the polar thickening in Hyoseris and may reflect some affinity with Aposeris and Rhagadiolus.

Progressive reduction in size of the polar thickening can also be seen elsewhere in the Leontodontinae. The lacunate polar thickenings of Hypochoeris radicata and Leontodon hirsutus are quite similar to that of Hyoseris radiata ssp. radiata. In Hedypnois pendula and several species of Hypochoeris (Figs. 28, 30), the reduction is manifested in a small polar plate that brings the ridges close together, with only a meager patch of vacant or sparsely spined tectum separating them. The occurrence of these features throughout the Leontodontinae (sensu Stebbins) supports Jeffrey's disposition of Aposeris and Hyoseris into his Hypochoeris subgroup. The narrow tripartite polar thickening occurs in many other genera of the Lactuceae, but the trilacunar polar plate, as far as is known, is

rare (e.g., Sonchus), thereby strengthening Jeffrey's case for placement of Hyoseris into the Hypochoeris Subgroup, a taxonomic unit comparable to the Leontodontinae of Stebbins.

While similar pollen morphologies seem to point to a possible relationship between Rhagadiolus and Aposeris, fruit structure and karyotype data support Rhagadiolus' alliance with Garhadiolus. Stebbins (1953) described the small, southern European genus, Rhagadiolus, as a highly specialized derivative of Garhadiolus (a small genus indigenous to southwestern Asia) in which the pappus has been lost and the mature achenes and inner involucral bracts are much elongated. Stebbins et al. (1953), found the karyotypes of the 2 taxa to be nearly identical, both possessing 10 medium-sized chromosomes with median or submedian centromeres. The karyotype of Aposeris is more similar to that of Hyoseris, i.e., Aposeris has 16 medium-large chromosomes with median centromeres; Hyoseris radiata has 16 medium chromosomes with median or submedian centromeres.

Pollen data from Rhagadiolus, Garhadiolus, and Hedypnois sheds little light on the disputed relationships among the three small genera. Both Hedypnois and Garhadiolus samples display a tendency to produce high percentages (40-50%) of tetracolporate grains, a fact that reveals little about their relationship except that both may be inclined toward cytologic abnormalities. But pollen morphology may well reflect the derivation of Rhagadiolus (small pollen with essentially no polar thickening) from Garhadiolus (large pollen with a spiny polar thickening) as proposed by Stebbins.

Cytological abnormalities and sculptural oddities in the pollen of Hedypnois complicate the already complex taxonomic problems in the genus. Nordenstam (1971) attempted to clarify some of the problems in Hedypnois through his studies of the cytology and morphology of 37 Aegean populations

of H. rhagadioloides. He found that within populations somatic chromosome numbers and morphological constancy was high, but interpopulational morphologies were quite variable, i.e., he identified 20 morphological groups in 37 populations. Chromosome numbers in different populations were 2n = 8, 13, 14, 15, 16, 17, and no correlation was found between external morphology and chromosome number, with one exception. Nordenstam postulated that the original basic number in the group may be x=4 and that the diploid and tetraploid populations are normally autogamous and thereby maintain a high degree of homozygosity. Occasional outbreeding then gives rise to new character combinations which eventually produce new evolutionary lines.

Pollen data in this study was gathered from entities that are termed Hedypnois cretica, H. monspeliensis, and H. pendula. However, the epithets cretica and monspeliensis have been widely used for material comparable to some of the H. rhagadioloides populations studied by Nordenstam. This illustrates the taxonomic and nomenclatural confusion that exists in the genus due to the widespread populational variation.

Hedypnois cretica pollen was distinct from most other taxa studied in several ways: (1) uniquely 'peaked' spines, (2) partially or entirely isolated polar thickening, and (3) all samples contained 40-50% tetracolporate grains along with the tricolporate grains. In light of Nordenstam's and Stebbins' (1953b) chromosomal data, the presence of the isolated polar thickening as a relatively stable character in the taxon may be interpreted as the by-product of a meiotic anomaly in what Stebbins termed "this extensive polyploid complex." Interestingly enough, a similar sculpturing phenomenon has been found in known amphiploid populations of Krigia of the subtribe Microseridinae (Tomb, pers. comm.). The presence of such a high percentage of tetracolporate grains in every

sample may well indicate the occurrence of unreduced gametophytes. The correlation of pollen dimorphism and polyploidy has been well documented (Chuang & Constance, 1969; Lewis, W. H., 1965). For example, Lewis (1964) found an increase in mean pollen sizes in known tetraploid populations of Oldenlandia corymbosa and a considerable percentage of 4-aperturate grains intermingled with the 3-aperturate grains normally found alone in diploid populations. Northington (1974) found ca 50% of the pollen of Pyrrhopappus grandiflorus, a tetraploid, to be tetracolporate. In view of these facts, the morphologic entity that H. cretica represents is likely to be a member of the polyploid complex of Hedypnois.

Hedypnois pendula and H. monspeliensis possess none of the aberrations typical of H. cretica. Their pollen is quite similar in size and morphology to Aposeris and Hyoseris, except in the occasional occurrence of fugitive spines in Hedypnois. Hedypnois pendula grains have a narrow polar thickening and enlarged paraporal ridge around the germinal aperture, similar to Aposeris. Hedypnois monspeliensis displays a tendency toward polar lacunae, much like Hyoseris.

The pollen data from Rhagadiolus, Garhadiolus and Hedypnois is admittedly meager and inconclusive. A more thorough sampling of pollen from each genus and a biosystematic revision of the cytologically problematic Hedypnois should preceed any definitive statement concerning the clarification of generic relationships by pollen morphology.

The morphological evidence presented here seems to support the proposal set forth by Jeffrey (1966), i.e., that Aposeris and Hyoseris have definite affinities for the Leontodontinae (sensu Stebbins). These data reveal the presence of similar distinguishing features in the pollen of Hyoseris, Hypochoeris, Leontodon, Aposeris, Rhagadiolus, and Hedypnois. Hence, the exclusion of Aposeris and Hyoseris from the Leontodontinae

seems inappropriate in light of pollen morphology. An investigation into the similarities and differences in floral morphology among the 9 genera by Sell (1975) also seems to support this conclusion.

Sell (1975) considered relationships among these 9 genera in terms of pappus structure, length of style arms and collecting hairs. He found that all genera of Jeffrey's Hypochoeris Subgroup possess long style arms and small collecting hairs, but differ in pappus structure. Like Stebbins, he recognized that Hypochoeris, Leontodon, Picris, and Urospermum typically have a pappus of plumose hairs, some of which are thickened at the base. Hedypnois and Hyoseris have a pappus of scales or simple hairs, some with swollen bases, and Aposeris and Rhagadiolus are epappose. Sell considered Hedypnois, Hyoseris, Aposeris and Rhagadiolus to be closely related to each other and, in fact, argues that they are conventionally separated only by characters of dubious relevance, a practice that is not consistent with the wide intrageneric variation that is accepted in their kindred genera, Leontodon and Hypochoeris.

In summary, the results of this study have served to document the cohesiveness of the Leontodontinae of Stebbins. The naturalness of this group is evidenced by the meager diversity found in pollen across the genera, with the exception of Hypochoeris in South America, where extensive adaptive radiation has occurred. In this study pollen proved to be of minimal use in identifying infrageneric section boundaries, and it was revealed that minor variations in sculpturing features are unstable geographically and at several subgeneric levels. This pollen data supports the alliance of Aposeris and Hyoseris with the Leontodontinae but is inconclusive in clarifying relationships among Rhagadiolus, Garhadiolus and Hedypnois.

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POLLEN MORPHOLOGY OF THE LEONTODONTINAE (ASTERACEAE:LACTUCEAE)

by

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(ASTERACEAE:LACTUCEAE)

ABSTRACT

Pollen of 42 species from nine genera was examined to (1) determine the variation in endo- and exomorphology, (2) analyze the utility of pollen morphology in elucidating taxonomic problems in the Leontodontinae, (3) apply pollen morphology in determining the taxonomic affinities of Hyoseris and Aposeris, thought by some to belong to the Leontodontinae, and (4) apply pollen morphology to the determination of the generic boundaries between Garhadiolus, Rhagadiolus and Hedypnois. SEM photographs were made for each taxon studied. Representatives of each genus were examined and photographed in the TEM. All taxa possessed echinolophate pollen except for the subechinate grains of some South American species of Hypochoeris. Variation in fine details of sculpturing was extensive at both inter- and intraspecific levels. Endomorphological organization was nearly identical in all taxa, with only the South American Hypochoeris again showing much diversity. These results demonstrated that the Leontodontinae is essentially a cohesive taxonomic unit, and supported the incorporation of Aposeris and Hyoseris into the subtribe, but do not conclusively indicate that Garhadiolus, Rhagadiolus, and Hedypnois should be merged.